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INCLUDING MITES AND TICKS

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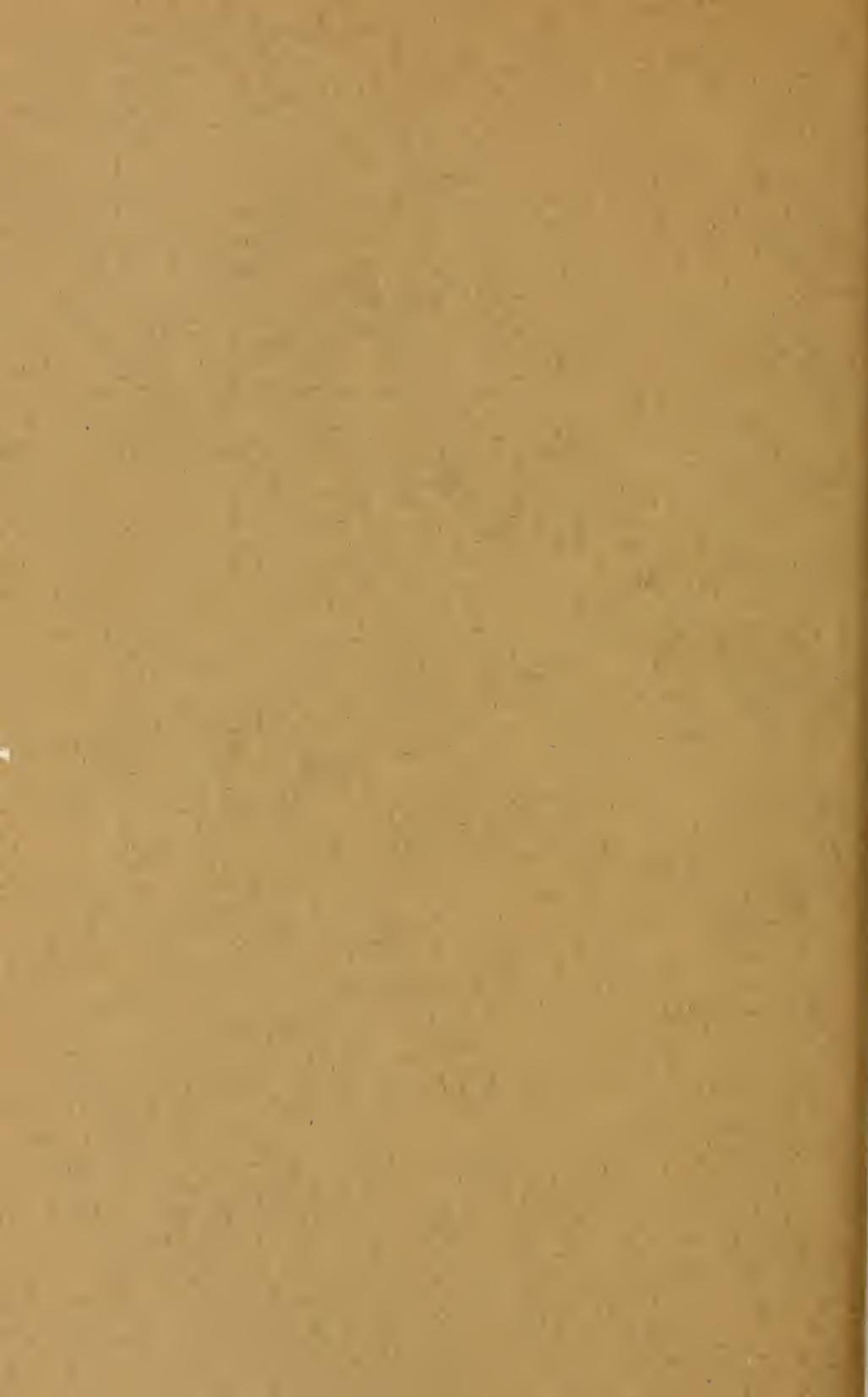
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Collaborator, Bureau of Entomology and Plant Quarantine  
U. S. Department of Agriculture



(PUBLICATION 3944)

CITY OF WASHINGTON  
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## CONTENTS

|  | PAGE |
|--|------|
| Introduction .....                               | 1    |
| I. General discussion of arachnid structure..... | 3    |
| The labrum and the epistome.....                 | 5    |
| The chelicerae .....                             | 6    |
| The pedipalps and the legs.....                  | 8    |
| The mouth and the preoral cavity.....            | 14   |
| The sucking organ, or so-called pharynx.....     | 15   |
| Comparison of Arachnida and Xiphosurida.....     | 16   |
| The stomach and digestion.....                   | 18   |
| II. The Palpigradi, or Microthelyphonida.....    | 19   |
| III. The Solpugida .....                         | 22   |
| IV. The Pedipalpida .....                        | 26   |
| V. The Ricinulei .....                           | 31   |
| VI. The Chelonethida, or Pseudoscorpionida.....  | 33   |
| VII. The Scorpionida .....                       | 39   |
| VIII. The Phalangida, or Opiliones.....          | 43   |
| IX. The Araneida .....                           | 51   |
| X. The Acarina .....                             | 61   |
| Notostigmata .....                               | 65   |
| Oribatoidea .....                                | 67   |
| Holothyroidea .....                              | 67   |
| Gamasides .....                                  | 69   |
| Ixodidae and Argasidae.....                      | 71   |
| Trombidiformes .....                             | 80   |
| Abbreviations used on the figures.....           | 86   |
| References .....                                 | 88   |

## INTRODUCTION

Inasmuch as feeding is the function of prime importance with all animals, it seems strange that no animals were originally endowed with organs of feeding other than an intake opening into the alimentary tract and a sucking device for the ingestion of nutrient material. Primitive animals, therefore, swallowed water or mud and depended for their subsistence on what organic matter might be therein con-

tained; and many modern animals still feed in this manner. It was left to evolution to produce accessory mouth structures for grasping, tearing, crushing, or chewing that would enable their possessors to get food in more concentrated form from plants or from the bodies of other animals. Since such organs are entirely different in the different groups in which they occur, it is clear that they have been independently developed. Thus we find in the polychaete worms a pair of eversible pharyngeal hooks serving as jaws, in the mollusks a rasping apparatus, in the sea urchins a complex apparatus with a set of movable prongs surrounding the mouth, in the mandibulate arthropods a pair of jaws fashioned from the bases of a pair of legs, and in the vertebrates jaws derived from gill arches.

The arachnids come from an ancestral line that never acquired organs for mastication, and even today they have no true jaws. The ancient trilobites probably were mud eaters; though they had plenty of legs, the legs were not structurally differentiated for special purposes, as in modern arthropods. The leg bases, it is true, were provided with strong, spiny mesal processes, but the latter did not meet along the midline of the body, and could have had little use as feeding organs other than perhaps that of stirring up the mud from which the animals obtained their food. Likewise, true jaws have not been developed in the Xiphosurida, though the first appendages of these animals have taken the form of a pair of pincers, the chelicerae, which serve for grasping and are said to be used for putting food into the mouth, and the coxae of the next five pairs of appendages are provided with large, spinous lobes, more highly developed than those of the trilobites, but still not adapted for efficient mastication of food. The mandibulate arthropods, however, have finally produced from the coxae of the second postoral appendages a pair of strong biting and chewing jaws.

Chelicerae are characteristic appendages of the Xiphosurida and the Arachnida. It is probable, therefore, but not a necessary assumption, that the arachnids and the xiphosurids inherited their chelicerae from some common progenitor. However, in the possession of chelicerae and legs, the primitive arachnids were well equipped for predatism and for terrestrial life; but, being without masticatory organs, they were forced to subsist on the liquids they could obtain from their prey. A liquid diet requires an ingestion pump, and, with all arachnids, a highly developed sucking apparatus constitutes the essential part of the feeding mechanism. Further structural evolution related to the feeding function of the Arachnida, therefore, should logically be in the direction of furnishing an efficient means

of conveying liquids to the mouth from the prey held and crushed in the chelicerae. A comparative study of the external arachnid feeding organs shows, in fact, that the mouth parts are elaborations of structures associated with the oral aperture to form a preoral food receptacle and conduit to the sucking pump. That such accessory feeding organs are not primitive becomes evident when we find that in each arachnid order a different kind of structure has been evolved. The several orders of the Arachnida, therefore, with respect to the feeding apparatus, have no serial relation to one another.

The entomologist who takes up a study of Arachnida obviously must readjust much of his anatomical outlook. Because insects and spiders are closely associated in nature, the study of arachnids has been a sort of sideline for entomologists; for which reason, probably, we find in the language of arachnology various terms that have been carried over from entomology, and, as might be expected, often applied to parts that have no homology with organs of insects. Particularly is this true with respect to the feeding organs. It is a part of the object of the present paper to eliminate entomological terms that have no proper application to arachnid anatomy. The vertebrate zoologist, of course, might justly contend that entomologists have no right to the many vertebrate terms that are given to insect structures. However, conceding that names may be legitimately borrowed, they should be applied consistently at least within any one phylum; otherwise definitions become conglomerations, and morphology is handicapped by a meaningless terminology.

## I. GENERAL DISCUSSION OF ARACHNID STRUCTURE

The fundamental structure of an arachnid is best understood from embryonic development. The young arachnid embryo (fig. 1 A, B), as the embryos of other arthropods, consists of a segmented or partly segmented body and a large head lobe (*HL*), which may be deeply cleft into lateral halves. Behind the cephalic lobe are the true somites, beginning with the somite of the chelicerae (*A, I*), which is followed by that of the pedipalps (*II*), and the four leg-bearing somites (*III-VI*). The embryonic head lobe of the arthropods always bears the labrum, the eyes, and the antennae if the latter are present, but the arachnids in common with the xiphosurids lack antennae, though these appendages were well developed in the trilobites. With development of the arachnid embryo, the labrum remains as a preoral, or supraoral, lobe of the head, but the ocular region extends posteriorly on the dorsum (*C, D, HL*) and becomes the eye-bearing

region of the back in the adult united with the tergal plates of following segments in the dorsum of the prosoma. The chelicerae become secondarily preoral, and in most cases the pedipalps take positions at the sides of the mouth.

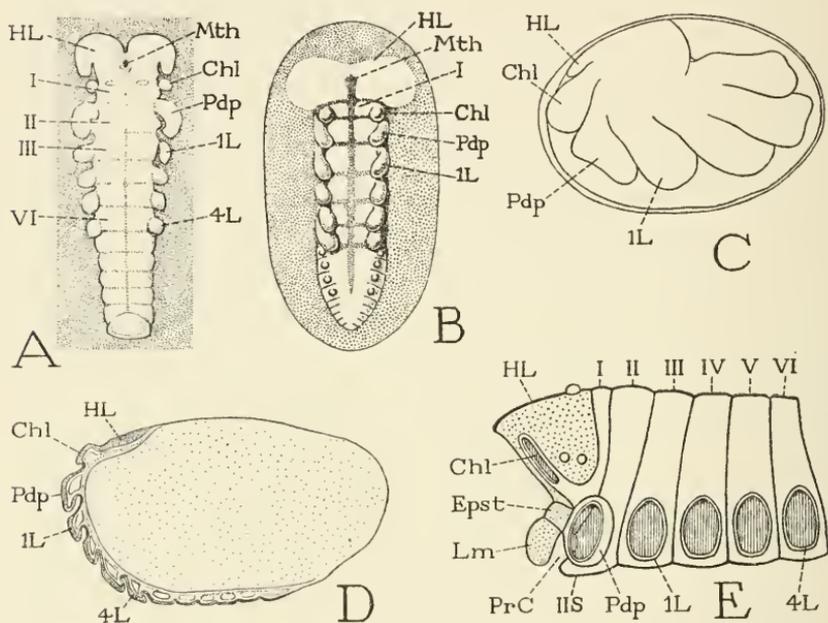


FIG. 1.—The prosomatic segmentation and appendages of Arachnida.

A, young embryo of *Euscorpis italicus* (Hbst.), extended in a plane, showing cephalic lobe (*HL*) and postoral somites with appendage rudiments (from Laurie, 1890). B, embryo of *Agelena labyrinthica* L. (from Balfour, 1880). C, young embryo of *Pediclopsis graminum* (Reuter) in the egg just before reversion, lateral (from Reuter, 1909). D, embryo of *Euscorpis italicus* (Hbst.), longitudinal section through germ band to one side of median plane, showing cephalic lobe (*HL*) extended posteriorly on dorsal surface (from Laurie, 1890). E, diagram of the approximate prosomatic segmentation of an adult arachnid; the primitive cephalic lobe (*HL*, stippled) forms the eye-bearing part of the back, the epistome (*Epst*), and the labrum (*Lm*), and is invaded on the sides by the primarily postoral chelicerae (*Chl*); the pedipalp coxae (*Pdp*) turned forward and united mesally with the epistome.

*Chl*, chelicera; *Epst*, epistome; *HL*, cephalic lobe of embryo; *I-VI*, postoral somites of prosoma; *IIS*, sternum of pedipalp somite; *1L-4L*, legs; *Lm*, labrum; *Mth*, mouth; *Pdp*, pedipalp; *PrC*, preoral food cavity.

The prosomatic segmentation of an adult arachnid, visualized from the known facts of anatomy and embryogeny, must be approximately as shown diagrammatically at E of figure 1. The part of the prosoma derived from the cephalic lobe of the embryo (*HL*, stippled) certainly includes the labrum (*Lm*), an epistomal region (*Epst*) differentiated at the base of the labrum, and the eye-bearing region of the back; it

therefore includes also the narrow median strip of the anterior body wall connecting the epistome with the carapace between the cheliceral bases. The somite of the chelicerae is postoral in the early embryo (A, B, *I*), but the chelicerae in their preoral transposition invade the anterior part of the primary cephalic region (E, *Chl*), while the sternal part of the cheliceral somite, except possibly in Palpigradi, becomes so reduced that it is not recognizable in the adult structure. The appendages of the second postoral somite, the so-called pedipalps (A, B, *Pdp*), retain the primitive position in the Palpigradi, but in the other arachnid orders they move forward to the sides of the mouth (E, *Pdp*), and generally their dorsal walls unite with the epistome (*Epst*). Either the sternal plate of the pedipalp somite (*IIS*) or some other structure forms a lower lip projecting in front of the mouth, and there is thus enclosed, between the pedipalp coxae on the sides and the labrum (*Lm*) above, a *preoral cavity* (*PrC*) for the reception of food.

The simple basic structure of the anterior part of an arachnid is well shown in a medium sagittal section, such as is represented diagrammatically at D of figure 2. The eye region of the dorsum, the intercheliceral space, the epistome (*Epst*), and the labrum (*Lm*) represent the cephalic lobe of the embryo. From the anterior margin of the back or carapace (*Cp*), the membranous front wall of the body (*a-c*) is reflected downward or obliquely backward, and bears the chelicerae (*Chl*) in their secondarily acquired supraoral position. Below the chelicerae the epistome (*Epst*) extends forward, and supports the labrum (*Lm*). The labrum is a free lobe, but the epistome lies between the pedipalp coxae and is generally united with their dorsal surfaces (A). Beneath the base of the labrum is the mouth (D, *Mth*). Projecting below the mouth is a lower lip, which may be the deutosternum (*IIS*), as shown in the diagram, or some other structure replacing the latter. Between the labrum and the lower lip, however the latter may be formed, is the preoral food cavity (*PrC*) enclosed laterally by the pedipalp coxae. The mouth leads directly into the sucking organ known as the pharynx (D, *Phy*), the dorsal dilator muscles of which (*dld*) are seen in the section to take their origins on the epistome (*Epst*). Modifications of these features occur in each of the arachnid orders, and are carried farthest in the Acarina, but they are clearly all derived from a simple basic structure.

*The labrum and the epistome.*—A labrum is a part of the standard equipment of all arthropods from trilobites to insects, and there is no apparent reason for calling the preoral lobe of an arachnid anything else than *labrum*. Yet we find the organ described under such

various names as "epipharynx," "camerostome," "rostrum," "lingula," "tonguelike process," and "styletlike process." The arachnid labrum is variable in size and shape in different groups, but it is always present as a lobe of some form projecting above and beyond the mouth at its base (fig. 2 A, *Lm*).

Proximal to the labrum, and supporting the latter, there is in most arachnids a distinct median plate (fig. 2 A, *Epst*) below the chelicerae. This plate has been regarded as a basal part of the labrum, or recognized as an individual structure under a variety of names, such as "clypeus," "epipharynx," "intermaxillary jugum," "subcheliceral plate." Since the plate in question is usually well separated from the labrum, and is postoral in position, it is evidently a part of the head wall; it corresponds with the *epistome* (clypeus) of mandibulate arthropods, and hence may be so named in the arachnids.

The arachnid epistome is not always distinctly separated from the labrum, and it may be more or less invaginated into the anterior body wall beneath the chelicerae, but it is to be identified by one or both of two characteristic relations to other structures. First, the plate is usually united with the pedipalp coxae, forming a bridge between their dorsal surfaces (fig. 2 A, *Epst*); and second, it *always* gives origin, either directly or by means of a basal apodeme, to the dorsal dilator muscles (D, *dld*) of the pharynx (*Phy*). In the xiphosurid *Limulus* also an epistomal plate (fig. 2 C, *Epst*) may be distinguished from the labrum (*Lm*); it here supports the chelicerae (*Chl*), and, while it is not united with the pedipalp coxae (*IICx*), it sends out a long arm on each side close to the coxal margin.

*The chelicerae.*—The chelicerae, being the first postoral appendages of the arachnid, must represent the corresponding appendages of the mandibulate arthropods, and these appendages are the second antennae of Crustacea, or their homologues, the vestigial premandibular appendages transiently present in some insect embryos. The homology of the arachnid chelicerae with the crustacean second antennae is accepted by Störmer (1944) as obvious from the facts of comparative anatomy, and is fully confirmed by the origin of the cheliceral nerves from the tritocerebral lobes of the brain, as shown by Holmgren (1920) and by Hanström (1928). The similar position of the arachnid chelicerae and the crustacean second antennae on the head is at once evident on comparison of a facial view of an arachnid (fig. 2 A) with that of an amphipod (E), and in the phalangid *Leiobunum* (fig. 16 A), as in the amphipod *Talorchestia* (fig. 2 E), a median bar (*f*) connects the epistome with the dorsal wall of the head. The chelicerae of the Chelicerata, therefore, are not the an-

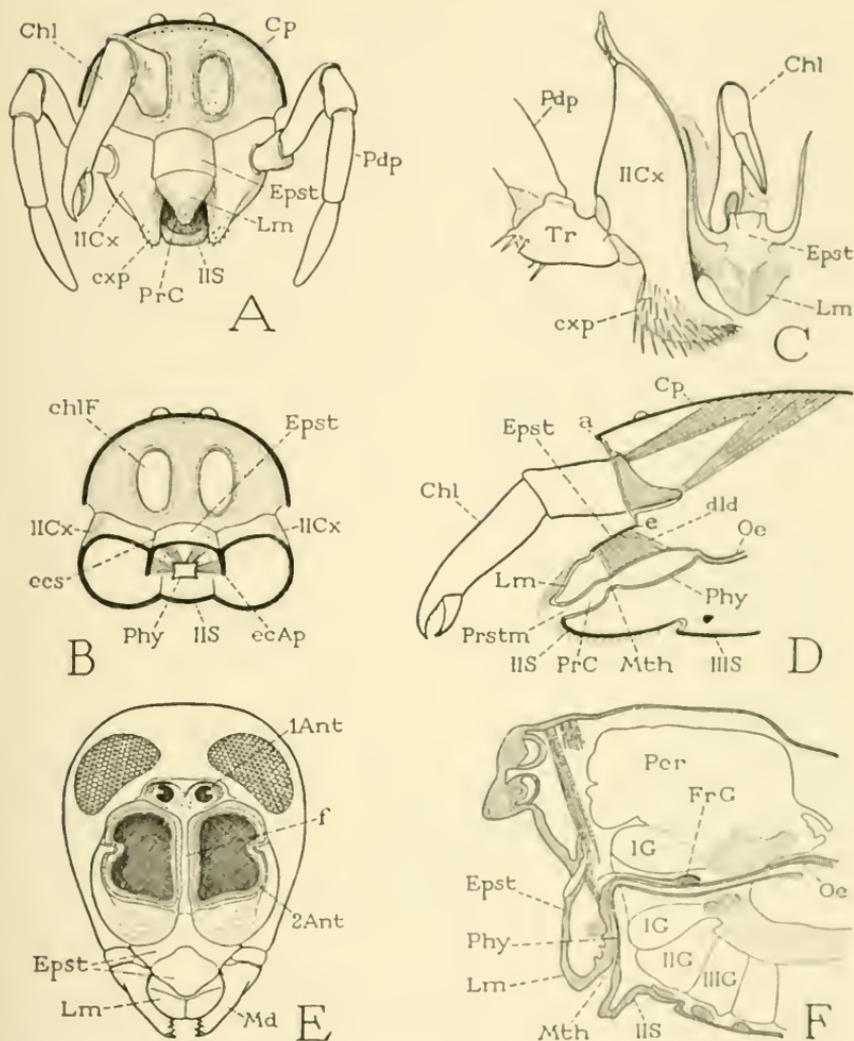


FIG. 2.—Cephalic structures of Arachnida, Niphosurida, and an amphipod crustacean.

A, anterior view of an arachnid, diagrammatic, the under lip represented as the pedipalp sternum (*IIS*) as in *Araneida*. B, the same with chelicerae removed and the mouth parts sectioned transversely behind the palps, exposing the pharynx and its muscles. C, *Limulus polyphemus* L., the mouth region, anterior, with right chelicera and base of right pedipalp. D, diagrammatic longitudinal section of A, showing the preoral cavity (*PrC*), pharynx (*Phy*), and dorsal pharyngeal muscles (*dld*) arising on the epistome (*Epst*). E, *Talorchestia longicornis* Say, amphipod crustacean, anterior view of head showing second antennae (*2Ant*) in position of chelicerae of an arachnid (*A, Chl*). F, *Trochosa* embryo, longitudinal section of anterior end, showing position of frontal ganglion (*FrG*) (from Holmgren, 1920, somewhat simplified).

tennules of mandibulate arthropods (fig. 2 E, *Ant*), as they were formerly thought to be, nor are they the mandibles, as some arachnologists still persist in calling them. Functionally, the chelicerae might be said to be the "jaws" of the arachnid, but their action is remote from the mouth and consists of grasping, holding, tearing, crushing, or piercing.

Some students of arachnid embryogeny, as Laurie (1890) and McClendon (1904), say the definitive preoral position of the chelicerae results from a posterior displacement of the mouth, while Reuter (1909) says that as the mouth moves caudad there is a simultaneous forward movement of the chelicerae. Since the mouth and the labrum retain their primitive positions at the anterior pole of the animal, the result, however produced, is the same as if the chelicerae had migrated anteriorly and dorsally around the mouth. In most cases the chelicerae come to lie entirely above the level of the epistome (fig. 2 A), and so close together that they reduce the area of the primary embryonic head lobe between them to a narrow vertical strip.

The chelicerae have the same essential structure and musculature in both the Xiphosurida (fig. 3 A) and the Arachnida (C). They are composed of three segments in *Limulus* (A), Palpigradi, Scorpionida (B), Phalangida (C), and many Acarina; they are two-segmented in Solpugida (F), Pedipalpida, Chelonethida, Araneida (G), and some Acarina. The uniformly simple structure of the chelicerae precludes the possibility of determining the homology of the cheliceral segments with the segments of a leg. The terminal segment is the "movable finger," which, except in Araneida (G), is usually opposed by an immovable process. The movable finger may be dorsal on the supporting segment, or it may be ventral, and in some forms lateral. The cheliceral pincer resembles the chela of a chelate pedipalp, but the movable finger of the chelicera has always both an opening and a closing muscle (fig. 3 A, D, E, F, G), while the movable finger of a pedipalp chela has only a closing muscle (fig. 5 E). When the chelicera is three-segmented (fig. 3 A, C), the middle segment is strongly muscled from the basal segment. The extrinsic muscles of the chelicerae arise on the dorsum of the prosona (fig. 3 C), there being no cheliceral muscles corresponding with the ventral muscles of the other appendages.

*The pedipalps and the legs.*—The pedipalps are the second postoral appendages of the Arachnida; they are thus the homologues of the *mandibles* of mandibulate arthropods; but arachnologists commonly call them the "maxillae," or at least they give this term to the coxae,

which usually are closely associated with the mouth. Though Hansen and Sørensen (1904), therefore, are morphologically correct in designating the pedipalp coxae "mandibles," the term is not appropriate in a functional sense, inasmuch as the pedipalp coxae do not form true jaws in any arachnid. Arachnology has the term *pedipalp* for the second pair of segmental appendages, and, though the latter are

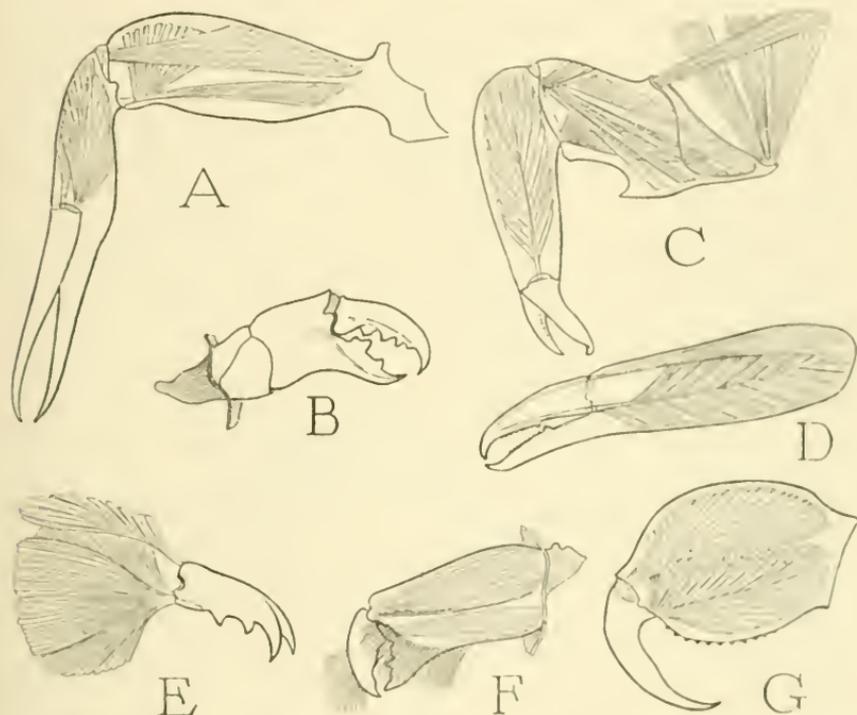


FIG. 3.—Structure and musculature of the chelicerae.

A, *Limulus polyphemus* L., Xiphosurida, left chelicera of a young specimen, lateral. B, *Pandinus* sp., Scorpionida, chelicera. C, *Leiobunum* sp., Phalangida, left chelicera and muscles, lateral. D, same, distal segments of chelicera, showing both muscles of movable finger. E, *Centruroides* sp., Scorpionida, movable finger of chelicera and its muscles. F, two-segmented chelicera of a solpugid. G, two-segmented chelicera of a spider, *Eurypelma hentzi* Chamb., lacking a fixed finger.

not always palpiiform, there would seem to be no good reason for calling them either maxillae or mandibles.

The coxae of the pedipalps in most of the arachnids are directed horizontally forward at the sides of the mouth (fig. 2A, *IICx*), and, as already noted, their dorsal surfaces are usually united with the epistome (*Epst*), which thus forms an intercoxal bridge. The lines of union are generally distinct grooves (B, *ecs*), which are

commonly inflected to form internal ridges or platelike *epistomocoxal apodemes* (B, *ecAp*). The coxal bases themselves may be produced into *coxal apodemes* (fig. 9 B, *cAp*) having lateral positions relative to the median epistomal apodeme (*eAp*) when the latter is present in the same species. Only in the Palpigradi do the pedipalps retain a postoral status and have no relation to the mouth (fig. 6 D, *Pdp*). It is of interest to note that in the mandibulate arthropods the mandibles have a relation to the epistome very similar to that of the pedipalp coxae to the epistome in the arachnids. In the pterygote insects with biting jaws, and the decapod crustaceans, for example, the mandibles have an anterior articulation on the epistome (clypeus), while the decapod jaw, in addition, has a long hinge line on the epistomal margin.

The telopodite of the pedipalp appendages may differ little from that of the legs, or it may be modified in various ways. Its adaptation in the male spider to form a sperm-carrying organ, having nothing to do with feeding, need not be considered here; but in the Scorpionida, Chelonethida, and some of the Pedipalpida the pedipalp is chelate, and with these arachnids the chelae become important adjuncts to the feeding function, since they serve for catching, holding, and crushing the prey. To understand the nature of the pedipalp chela it will be necessary to study the structure and musculature of the distal segments of an ordinary walking leg.

The simplest structure of the end segment of an arthropod limb is seen in the legs of malacostracan Crustacea in which the appendage terminates with a clawlike segment, called the dactylopodite, movable by levator and depressor muscles arising in the segment proximal to it, which is the propodite, or tarsus. The legs of *Limulus* have a similar structure (fig. 4 F) though here the dactylopodite, or pretarsus (*Ptar*), forms the movable finger of a chela. Among the Arachnida a simple, clawlike end segment of the leg occurs in some of the Phalangida, as in *Leiobunum* (B, *Ptar*); but more commonly the pretarsus of the walking legs bears a pair of lateral claws, or *ungues* (A, *Un*), while the median claw is reduced to a toothlike dactyl (*Dac*) on the short base of the segment. Whatever the structure of the pretarsus may be, however, two tendons are always attached to its base (A, B, *lvt*, *dpt*), one giving insertion to a levator (extensor) muscle, the other to a depressor (flexor) muscle. Even though the claws be greatly reduced or entirely absent, and the pretarsus become indistinguishable from the end of the tarsus, the two pretarsal tendons and their muscles may be retained, as in the slender first legs of Thelyphonidae. The levator muscle of the pretarsus in

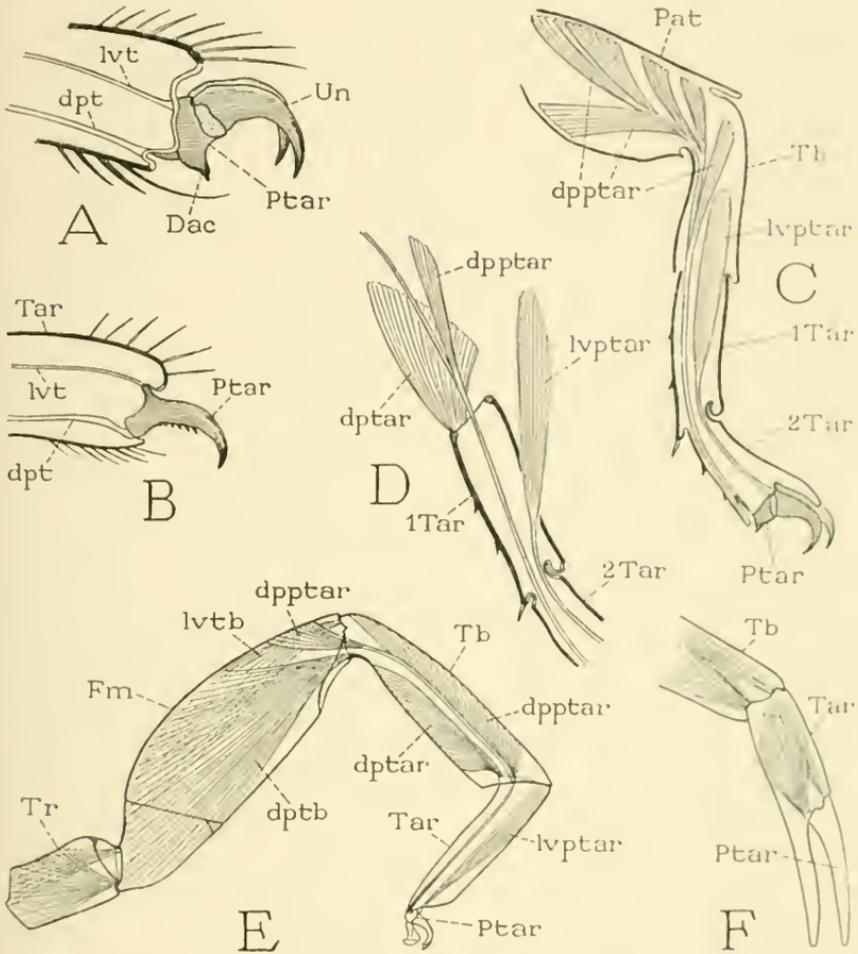


FIG. 4.—Segmentation and musculature of the arachnid leg, and pretarsus of *Limulus*.

A, *Mastigoproctus giganteus* (H. Lucas), Pedipalpida, end of a leg, pretarsus with a median claw (*Dac*) and two lateral claws (*Un*). B, *Leiobunum* sp., Phalangida, end of pedipalp tarsus, with simple clawlike pretarsus. C, *Pandinus* sp., Scorpionida, distal segments of leg showing distribution of pretarsal muscles. D, *Centruroides* sp., Scorpionida, base of tarsus, showing presence of only a single tarsal muscle, a depressor (*dptar*), arising in tibia. E, *Atemnus politus* (Simon), Chelonethida, fourth leg and muscles, only one muscle (*dptar*) on base of tarsus (from Chamberlin, 1931). F, *Limulus polyphemus* L., Xiphosurida, chela of a leg, both muscles of pretarsus arising in tarsus.

*Dac*, dactyl (median claw); *dpptar*, depressor muscle of pretarsus; *dpt*, depressor tendon of pretarsus; *dptar*, depressor of tarsus; *dptb*, depressor of tibia; *Fm*, femur; *lvptar*, levator of pretarsus; *lvt*, levator tendon of pretarsus; *lvtb*, levator of tibia; *Pat*, patella; *Ptar*, pretarsus; *Tar*, tarsus, *1Tar*, *2Tar*, first and second tarsal subsegments; *Tb*, tibia; *Tr*, trochanter; *Un*, unguis (lateral claw).

some arachnids arises in the tarsus (fig. 4 E, *lvptar*), in others it takes its origin in the tibia (C). The larger and stronger depressor muscle has no connection in the tarsus, but a branch of it arises in the tibia, and one or several branches in the patella (C, *dpptar*), unless a patella is absent, in which case the upper part of the muscle arises in the femur (E, *dpptar*).

The tarsus of an arachnid leg may be a simple segment (fig. 4 E, *Tar*), or it may be divided into two or more subsegments, or tarsomeres (C, *1Tar*, *2Tar*). No muscles are ever present between tarsomeres. It is important to note, furthermore, that the tarsus itself has only one muscle, a depressor, which arises in the tibia (D, E, *dptar*). The character of the distal musculature of the leg, therefore, will serve to identify the pretarsus, the tarsus, and the tibia when the identity of these segments is not otherwise clear.

The chelate arachnid pedipalp (fig. 5 D) has only six segments, of which the last is the movable finger of the chela, and might therefore appear to be a clawlike pretarsus. A study of the musculature, however, shows that the finger is movable by *only one muscle*, and that one a depressor (E, G, *dptar*), which thus corresponds with the single muscle of the tarsus of a leg (fig. 4 D, E, *dptar*). In the nonchelate pedipalp of one of the amblypygous Pedipalpida, *Trithyreus* (fig. 5 A), it is shown by Börner (1904) that the small pretarsus (*Ptar*) has the usual pretarsal musculature (*lvptar*, *dpptar*). In the Thelyphonidae of the same order the pedipalp is chelate (C) and there is no distinct pretarsus, but attached within the apex of the movable finger Börner finds the tendon of a depressor muscle, from which fact he logically contends that the movable finger is the tarsus and pretarsus combined. According to Barrows (1925) two tendons are attached in the pedipalp finger in *Mastigoproctus* (B), one giving insertion to a small muscle arising in the proximal segment (*Tb*), the other to a muscle from the next segment (*Pat*). Some over-hardened specimens of *Mastigoproctus* examined by the writer appear to confirm Barrow's statement. By comparison with a leg, therefore, the movable finger of the pedipalp chela is the combined tarsus and pretarsus (B-G), and the proximal segment, or "hand," containing the single depressor muscle of the finger, is the tibia (*Tb*), while the segment supporting the chela is the patella (*Pat*). Both Börner and Barrows regard the basal segment of the chela as a proximal segment of the tarsus, but this interpretation is clearly not in accord with the musculature, since the single muscle of the finger is evidently the tarsal muscle of a leg, and tarsal subsegments are never interconnected by muscles.

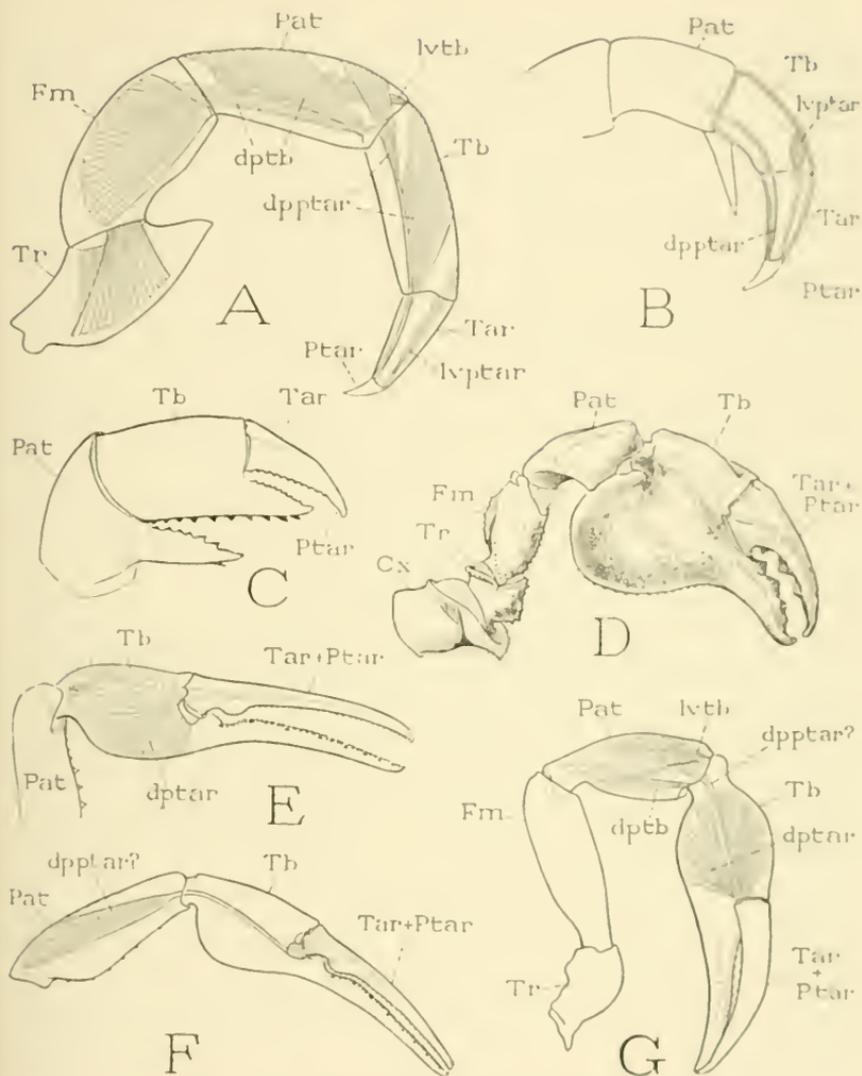


FIG. 5.—Segmentation of the chelate pedipalp.

A, *Trithyreus cambridgei* (Thor), Pedipalpida-Uropygi-Schizopeltidia, pedipalp and muscles (from Börner, 1904, but "tibia" and "first tarsal segment" of Börner here interpreted as patella and tibia respectively). B, *Mastigoproctus giganteus* (H. Lucas), Pedipalpida-Uropygi-Holopeltidia, distal segments of pedipalp (from Barrows, 1925, but "tibia" and "metatarsus" of Barrows here interpreted as patella and tibia). C, same, patella and chela of pedipalp. D, *Pandinus* sp., Scorpionida, pedipalp. E, *Centruroides* sp., Scorpionida, chela, showing depressor muscle of tarsus in basal segment. F, same, showing muscle from patella to base of movable finger. G, *Dasycheres inquilinus* Chamb., Chelonethida, pedipalp (from Chamberlin, 1931, but "tibia" of Chamberlin interpreted as the patella).

Lettering as on figure 4.

In the scorpion (fig. 5 E) the basal segment of the chela (*Tb*) contains a great mass of depressor muscles (*dptar*) of the movable finger, divided into three distinct bundles of fibers, two of which are lateral and one ventral. Above the ventral muscle runs a strong median tendon (F), attached distally on the base of the finger, and giving insertion proximally to a large, dense, fusiform muscle (*dpptar?*) in the patella (*Pat*). Functionally this muscle is an effective depressor of the finger, but its origin in the patella suggests that it represents the patellar branch of the depressor of the pretarsus in the scorpion leg (fig. 4 C, *dpptar*). A similar muscle is shown by Chamberlin (1931) to be present in the pedipalp of the pseudoscorpion (fig. 5 G, *dpptar?*).

*The mouth and the preoral cavity.*—The mouth of an arthropod embryo lies between the base of the labrum and the venter of the first postoral somite. Though a labrum is almost always present and overhangs the mouth, the sternal region of the postoral somite is seldom to be identified in the adult structure.

In the arachnid order Palpigradi the mouth is on the end of a snoutlike cone projecting from between the bases of the chelicerae (fig. 6 B, D), and the pedipalps are entirely postoral in position (D, *Pdp*). The mouth cone is formed by a dorsal plate, clearly the labrum (*Lm*), and a similar ventral plate. The ventral plate cannot possibly be referred to the segment of the postoral pedipalps, and is therefore most reasonably regarded by Börner (1902) as the sternum of the cheliceral segment (*IS*), retained in the Palpigradi, but lost, or not recognizable as such, in any other arachnid.

Among the other arachnid orders there is nearly always present an under-lip structure, but it never corresponds with the suboral plate of the Palpigradi. In the Araneida the functional under lip is the projecting sternum of the pedipalp segment; in the Phalangida it is the sternum of the first leg segment; in the Scorpionida it is formed by coxal lobes of the first and second legs; in the Thelyphonidae and Ricinulei it is the united coxae of the pedipalps; in most of the Acarina it is a long lobe, known as the hypostome, produced from the united pedipalp coxae. In these orders the pedipalp coxae are turned forward at the sides of the mouth so that there is enclosed a preoral cavity between the labrum above, an under lip below, and the pedipalp coxae on the sides.

That the external feeding organs of the Arachnida constitute a "beak," or are derived from such a structure, seems to be an idea prevalent with many writers. Bernard (1895, p. 391), for example, in discussing what he calls the "beak" of the Solpugida, says: "The

possession of this organ in such diverse Arachnids as *Galeodes*, *Chernes*, and *Thelyphonus*, and the easy deduction of the mouth-parts of Spiders, *Scorpio* and *Phrynus*, from such an organ, render it almost certain that a beak was present in the original Arachnid." Pocock (1902), on the other hand, rejects this idea. He shows that the so-called "beaks" in the different arachnid orders do not have the same composition, and he points out "that there is no difficulty in regarding all these various kinds of 'beaks' as specialized organs resulting from the presence of a camarastome or labrum, and the need for a lower lip or suboral gutter to prevent the loss of nutritive fluids and to guide them into the alimentary canal." The labrum overhanging the mouth, Pocock contends, is the primary structure associated with the oral aperture, since a labrum in some form is found in all the arachnids. The lower lip, on the other hand, is a secondary structure, as is shown by the different ways in which it is formed (as above enumerated). The association of the pedipalp coxae with the upper and lower lips then completes whatever may be called a "beak," or "rostrum," but clearly the structure thus composed is a secondary formation adaptive to the liquid-feeding habits of the arachnids.

The intercoxal antechamber of the mouth is an important part of the arachnid feeding apparatus, and becomes variously modified in the several orders; it serves for the reception of food from the chelicerae, and as a mixing bowl with those arachnids that practice extraoral digestion. This preoral food chamber, however, is not a "buccal cavity," "buccal canal," or "Mundhöhle," as it is commonly called, since a buccal cavity, in any proper anatomical sense, should be within the mouth and not outside of it. The arachnid food receptacle is a *preoral cavity*, so termed by Pavlovsky and Zarin (1926), or the "Mundvorraum" of some German writers. It is entirely comparable to the preoral food cavity of an insect between the enclosing mouth parts.

*The sucking organ, or so-called pharynx.*—The mouth of the arachnid (fig. 2 D, *Mth*), lying at the inner end of the preoral cavity beneath the base of the labrum, opens directly into the sucking apparatus known as the *pharynx* (*Phy*). This organ varies much in size and shape in the different arachnid orders, but it is always provided with dilator muscles, and usually with constrictor muscles, and thus is capable of a sucking action. The dilators include dorsal and lateral or ventrolateral groups of fibers converging on the pharyngeal walls (fig. 2 B, *Phy*). The dorsal dilators (*D*, *ddl*) always take their origins on the epistomal plate (*Epst*) or on a basal apodeme of the epistome; the lateral dilators arise on apodemal inflexions between the epistome

and the pedipalp coxae (B, *ecAp*), on apodemes of the coxae, or on the coxal walls.

The sucking organ of the arachnids, with its dorsal dilator muscles arising on the epistome, is suggestive of the sucking pump of liquid-feeding insects, with its dilator muscles arising on the clypeus. Furthermore, the organ in each case is *anterior* to the frontal ganglion and its brain connectives. The frontal ganglion of the arachnid lies on the dorsal surface of the oesophagus (fig. 2 F, *FrG*), but since the oesophagus (*Oe*) penetrates the central nerve mass, the ganglion, as shown by Holmgren (1920) and by Hanström (1928), is buried within the surrounding tritocerebral lobes of the brain (F, *IG*).

The usual sucking organ of the insects, with dilator muscles from the clypeus, is *not the pharynx*; it is a derivative of the preoral food cavity, while the true pharynx is a part of the stomodaeum and lies behind the frontal ganglion. The sucking organ of the arachnids is usually said to be the first part of the stomodaeum, and is therefore called the pharynx. According to Wagner (1894), however, the sucking apparatus as developed in *Ixodes* is a secondary invagination added to the primary stomodaeal invagination, "ein neues Theil des Stomodeums, welcher die Anlage für den Saugapparat bildet," the walls of which become hardened and give attachment to the dilator muscles. The primary stomodaeal invagination, Wagner says, forms the narrow oesophagus. There is therefore reason to believe that the so-called pharynx of the arachnids is a secondary derivative of the preoral cavity, as is the preoral cibarial sucking pump of the insects. Though the arachnid organ is usually well differentiated in structure from the functional preoral cavity, it is in some cases, as in the Thelyphonidae and Araneida, practically continuous with the latter, and in the Chelone-thida most of the dilator muscles arising on the epistome are inserted on the dorsal wall of the preoral cavity. To avoid confusion with current nomenclature, however, we may continue to call the sucking organ of the arachnids the "pharynx."

The oesophagus is always a narrow tube, which, after leaving the pharynx, traverses the central nerve mass on its way back to the mesenteron. Just before entering the latter it usually enlarges to form a small second, proventricular sucking organ, the so-called "stomach pump," or "Saugmagen."

*Comparison of Arachnida and Xiphosurida.*—A comparison of the arachnids with the xiphosurids shows that there is little in common between the two groups with respect to the feeding organs or the method of feeding. In the Xiphosurida the coxae of the first five pairs of postcheliceral appendages have large spiny mesal lobes op-

posed to each other from opposite sides in such a manner as to enclose a triangular space between them with the mouth at its apex. The coxal spines converge forward toward the oral aperture. The food of the xiphosurids consists principally of worms and small mollusks. The prey is said by Lockwood (1870) to be grasped by the leg pincers and brought beneath the body, where it is lodged between the coxae. The coxae then close against it from the sides and with their spines push it forward to the mouth, into which it is inserted by the legs. Lockwood says the food is rasped and comminuted by the coxal spines, but Schlottke (1935) observes that when *Limulus* is fed pieces of fish, the pieces are gulped down entire, though he admits that shellfish may be crushed by the coxae. In any case, the ingested food is ground up in a strong proventricular gizzard before it is passed into the stomach.

By contrast with the xiphosurids the Arachnida are essentially liquid-feeders. The prey is caught by the chelicerae, or the pedipalps if these appendages are chelate, crushed or lacerated, and held in the chelicerae while the exuding body liquids are sucked out. The arachnids have no chewing organs. The pedipalp coxae, or also the coxae of the first legs, may have lobes functionally associated with the mouth, but they are not masticatory in function, nor do they resemble the coxal lobes of *Limulus*. In the Palpigradi there are no such lobes, and the pedipalps are entirely postoral. If, therefore, the palpigrade mouth structure represents a primitive condition among the Arachnida, as it appears to do, the arachnid feeding apparatus has been evolved quite independently, and has no relation to the feeding organs of modern Xiphosurida. All the arachnids have an efficient sucking pump for the ingestion of liquids, but they have no grinding organ such as the gizzard of *Limulus*. In general, only food in liquid form can pass the arachnid ingestion apparatus, since usually the entrance is guarded by straining fringes of hairs, and the oesophagus is a very slender tube from the pharynx to the stomach: blood corpuscles and spores, however, may be carried in suspension, and in the phalangiids, it is said, even hard fragments of the food are to be found in the stomach. With some of the arachnids, particularly the Araneida, the availability of the tissues of the prey is increased by the practice of extraoral digestion. The arachnids possess salivary glands, and large excretory organs, the so-called "Malpighian vessels," discharging through the anus; the xiphosurids have no salivary glands, and no excretory organs connected with the alimentary canal.

Considering the differences above enumerated between the Arachnida and the Xiphosurida, it is evident that the two groups represent

separate lines of evolution within the Chelicerata, and that the arachnids have not been derived from any *Limulus*-like progenitor. The xiphosurids, on the other hand, show unmistakable affinities to the trilobites, whose habits of living must have been similar to those of *Limulus*.

*The stomach and digestion.*—The greater part of the food tract of the arachnids is formed from the mesenteron, including the stomach proper, the anterior part of the intestine, and the excretory vessels known as “Malpighian tubules” that open with the intestine into a terminal proctodaeal cloaca. The stomach consists of a central canal and of radiating diverticula, which latter may be few and sacklike, or numerous and tubular. The earlier workers on the digestive processes of Arachnida, including Plateau (1877) and Bertkau (1884), regarded the stomach diverticula as digestive glands, but it was shown by Bernard (1893) and Berlese (1897) that the diverticula constitute the digestive region of the stomach. These writers, furthermore, claimed that digestion with the Arachnida takes place *intracellularly* in the epithelium of the diverticula, and their contention has been substantiated by the more detailed studies of later investigators, including Oetcke (1912), Roesler (1934), Schlottke (1934), Bader (1938), and Frank (1938). Pavlovsky and Zarin (1926) showed that the digestive enzymes in the scorpion, including amylase, lipase, and proteinases, are formed only in the stomach diverticula.

The epithelium of the stomach diverticula consists of two distinct kinds of functionally active cells; namely, *secretory cells*, or “ferment” cells, and *digestive cells*. Prior to feeding, the secretory cells are filled with globules of secretion products; the digestive cells are practically devoid of inclusions. After feeding, the secretory cells discharge their contents into the lumina of the diverticula, while the digestive cells soon begin to show loose masses of material in their cytoplasm, which later condense into dark-staining globules. In a starved animal, secretion products are again formed in the secretory cells, but the globules of the digestive cells gradually disappear. From these histological phenomena it is deduced that the globules formed in the digestive cells are masses of ingested food material, which is finally digested in the cells and absorbed. Confirmatory evidence is seen in the fact that granules of excretory matter accumulate in the distal parts of these cells, which in most cases are discharged into the stomach lumen by constriction and separation of the ends of the cells. In those Acarina that have no intestinal outlet from the stomach, the excretory granules remain in the epithelial cells.

Different investigators are not entirely in accord as to the part

played in digestion by the secretion of the secretory cells. Oetcke (1912) believed that the tissues of the prey are first dissolved by secretion of the salivary glands, and that the liquefied food is then taken into the digestive cells, where it is digested by the digestive secretion absorbed from the secretory cells. According to Roesler (1934), Schlottke (1934), Frank (1938), and Bader (1938), however, a preliminary digestion by enzymes from the secretory cells takes place in the lumina of the diverticula, after which the process is completed within the digestive cells (presumably by enzymes formed in the latter). It thus appears that only the final phase of digestion is intracellular.

The digestive processes of *Limulus*, as described by Schlottke (1935), are similar to those of the Arachnida. After the food has been ground up in the proventricular gizzard it is passed into the central lumen of the stomach, where it is deluged with digestive fluid from the many-branched diverticula, containing protease, carboxypolypeptidase, amylase, and lipase. In a state of "predigestion" the liquefied food is then forced into the end branches of the diverticula and absorbed by the digestive cells, within which a dipeptidase completes the process of digestion. Similarly in the Pycnogonida Schlottke (1933a) has shown that digestion takes place intracellularly in the absorptive cells of the stomach diverticula. The ingested food of the pycnogonids, however, Schlottke says, contains no particles and no recognizable fragments of the tissues of the prey, a fact suggesting that the secretion cells of the stomach, which become active before feeding, must play some part in the liquefaction of the food, since the filtering apparatus of the stomodaeum could hardly be supposed to reduce the food to a liquid condition by mechanical action.

Some arachnids, particularly the Araneida, are well known to practice extraoral digestion. The solvent fluid discharged from the mouth has been generally supposed to be a product of the salivary glands, but the amount of the liquid exuded from the mouth is often so great that it would seem more probable, as contended by Kästner (see Gerhardt and Kästner, 1937), that it comes from the stomach diverticula.

## II. THE PALPIGRADI, OR MICROTHELYPHONIDA

The members of this order, comprising about 20 known species, are minute creatures, mostly tropical or subtropical in distribution, with species in the Mediterranean region of Europe, and in Texas and California of the United States. The pedipalps of these arachnids

(fig. 6 A) are leglike and have no association with the mouth; the first legs are long and slender; the relatively large, segmented abdomen terminates in a multiarticulate flagellum. The name Palpigradi approximately expresses the fact that the palps are leglike and used for walking; the name Microthelyphonida implies a resemblance to the Thelyphonidae of the Order Pedipalpida in the possession of a jointed tail, but otherwise there is no likeness between the two groups. Though the second name antedates the other by a matter of two years, the first is preferable for brevity and significance.

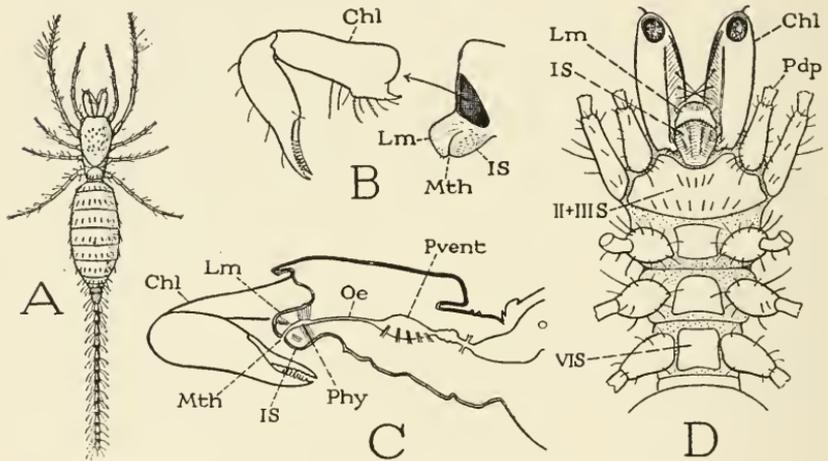


FIG. 6.—Palpigradi.

A, *Koenenia mirabilis* Grassi (from Hansen and Sørensen, 1897). B, same, anterior end of body with mouth cone and detached left chelicera (from Hansen and Sørensen, 1897). C, *Prokoenenia wheeleri* (Rucker), median section through mouth cone and prosoma (outline from Rucker, 1901). D, *Koenenia mirabilis* Grassi, prosoma and bases of appendages, ventral (from Börner, 1901).

The structure of the palpigrades is known principally from the work of Hansen and Sørensen (1897), Börner (1901, 1902), Wheeler (1900), and Rucker (1901, 1903). The last two writers record also something of the habits of *Prokoenenia* (*Koenenia*) *wheeleri* (Rucker). Wheeler suggested that this species, found in Texas, feeds on the eggs of *Campodea* and *Japyx*, with which it is associated in nature under stones where there is a sufficient degree of moisture; Rucker (1903) says that the alimentary canal contains nothing but material resembling yolk particles, and is "admirably constructed for such an illegitimate practice as egg-sucking."

With respect to the feeding organs the Palpigradi are the simplest of the arachnids. The relatively large, three-segmented chelicerae (fig. 6 B, *Chl*) arise at the base of a snoutlike cone bearing the mouth

(*Mth*), and are thus but little preoral in position. The leglike second appendages, corresponding with the pedipalps of other arachnids, lie entirely behind the mouth (*D. Pdp*), and are connected with a large ventral plate (*II+IIIS*) that would appear to be a combination of the deutosternum and the tritosternum, since it bears both the second and the third pairs of appendages. The pedipalps are said by Rucker (1901) to be used in common with the posterior three pairs of legs as locomotor organs, while the long slender first legs are held aloft and waved about in the manner of palps. The pedipalp coxae, having no association with the mouth, are in no way involved in the function of feeding.

The snoutlike cone that bears the mouth of the palpigrades (fig. 6 B, *Mth*) has no duplicate in any other arachnid order. The part above the transverse mouth slit is evidently the labrum (*Lm*), or labrum and epistome. The suboral part (*IS*) is interpreted by Börner (1902) as the prosternum, that is, the sternum of the cheliceral segment; there is, in fact, no other structure to which it might be referred, and the close association of the chelicerae with the base of the cone is entirely in harmony with this view. If, therefore, the mouth of the palpigrades lies between the labrum and the sternum of the first post-oral somite, we see here an embryonic condition retained in no other modern adult arthropod. The complete dissociation of the pedipalps from the mouth, Kästner (1932b) says, is known otherwise than in the Palpigradi only in the Jurassic fossil arachnid *Sternarthron* of Haase (1890). Haase, himself, regarded the likeness of *Sternarthron* to the living Palpigrada as so close that he included it in this order.

The mouth cone of the Palpigradi suggests the proboscis of the Pycnogonida, which projects below the chelicerae and between the pedipalps, but the pedipalps arise, as in the Palpigradi, from a sternal plate behind the base of the proboscis. The pycnogonid proboscis, however, has an elaborate innervation from a number of apical ganglia that are connected dorsally with the brain by a single nerve trunk, and ventrally with the suboesophageal ganglion by two nerve trunks (see Wirén, 1918, and Hanström, 1928). If the apical ganglia, as Hanström contends, represent the frontal ganglion, this ganglionic complex of the pycnogonids has quite a different relation to the stomodaeum within the proboscis than has the frontal ganglion of the arachnids. Moreover, the innervation of the lower half of the pycnogonid proboscis from the pedipalp centers of the suboesophageal ganglion does not conform with the idea that this part of the organ represents the sternum of the cheliceral segment. It seems probable, therefore, that the pycnogonid proboscis is a structure independ-

ently developed, and unrelated to the mouth cone of the Palpigradi.

If the mouth structure of the Palpigradi really is primitive for the arachnids, then there can be no direct relationship of the Arachnida to the Xiphosurida, and the coxal lobes of the higher arachnids must have been developed quite independently of those of the xiphosurids.

The mouth of *Prokoenenia wheeleri*, Rucker (1901) says, "leads into a strongly-chitinized pharynx (fig. 6 C, *Phy*). This in turn runs into a very delicate oesophagus (*Oe*) which penetrates the cephalothoracic nerve mass, only to dilate immediately into a pouch-like sucking stomach" (*Pvent*). The pharynx is shown in one of Rucker's figures to have dilator muscles arising dorsally on the upper wall of the mouth cone, and ventrally on the lower wall. According to Börner (1902), the walls of the pharynx contain a dorsal plate, which is the under surface of the labrum, and a ventral plate, which is the upper surface of the suboral prosternum. The "pharynx" of the Palpigradi would thus appear to be a specialized preoral cavity; yet Kästner (1932b) ascribes it to the stomodaeum (Vorder-Darm).

### III. THE SOLPUGIDA

Most conspicuous of the feeding organs of the solpugids are the huge, two-segmented chelicerae (fig. 7 C), directed straight forward from the anterior section of the body (A), which latter appears to be constructed particularly for their support, though it carries also the pedipalps and the first pair of legs. The solpugids are said to employ principally the last three pairs of legs for locomotion, the first legs being often used as accessories to the palps for catching and holding the prey. The coxae of the pedipalps and those of the first legs are firmly united on each side (B, *IICx*, *IIICx*), and the two pairs are supported on a single T-shaped sternal plate, which would appear to represent the deutosternum and the tritosternum combined. The narrow, deeply channeled anterior part of the plate (*IIS*) lies between the pedipalp coxae; the posterior part is a transverse bar (*IIIS*) behind the first leg coxae. The following three sterna are individual plates, though each is divided by a median groove that forms an internal ridge. That these plates are sterna and not the coxae of the legs is shown by the presence of large apodemal structures arising from them, and by the fact that the legs have a full complement of segments, including two trochanters.

The pedipalps arise entirely behind the mouth region (fig. 7 B), as they do in the Palpigradi, but in the solpugids their large coxae diverge forward beneath the chelicerae (B), and each is produced

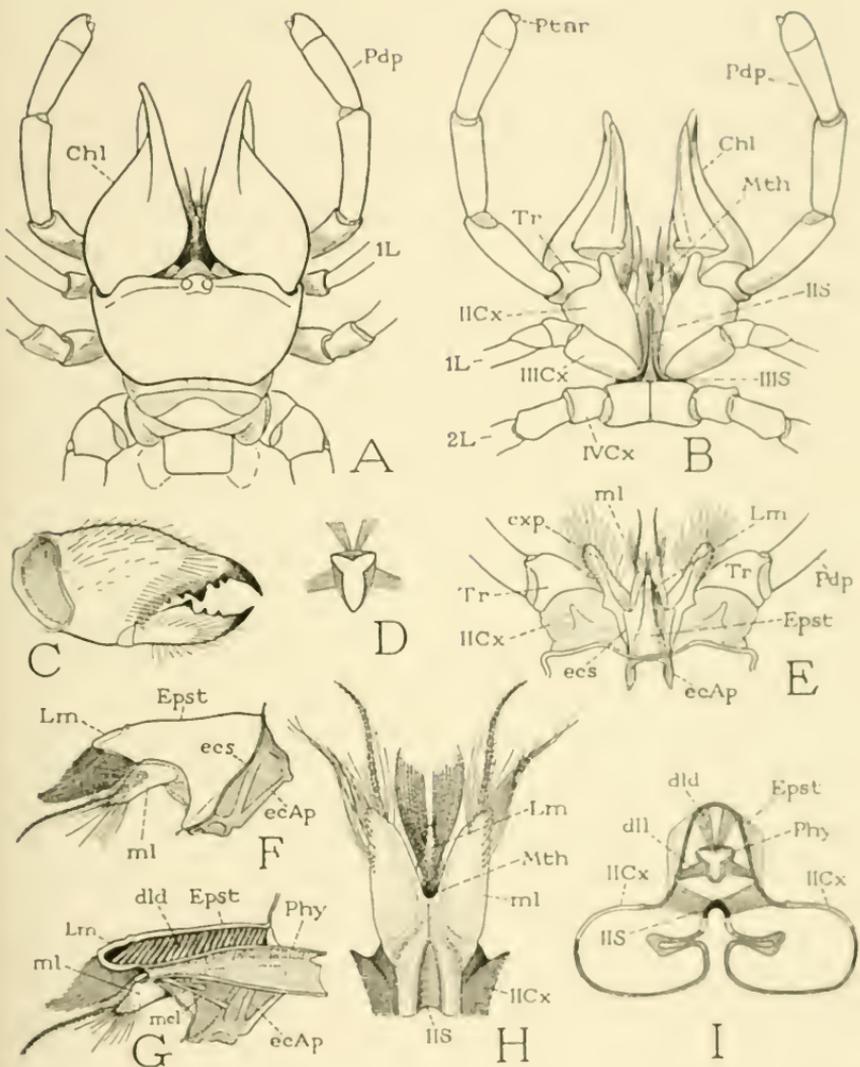


FIG. 7.—Solpugida (unidentified species).

A, prosoma and appendages, dorsal. B, anterior part of same, ventral. C, left chelicera, mesal. D, cross section of posterior part of pharynx, with muscles. E, mouth region and bases of pedipalps, dorsal. F, epistome and labrum detached from pedipalp coxae, exposing epistomocoxal apodeme (ecAp) of left side. G, median longitudinal section through epistome, labrum, and pharynx. H, mouth region, ventral. I, cross section through epistome, pedipalp coxae, and anterior part of pharynx.

into a thick, blunt process (E, *cxp*) projecting mesad of the trochanter (*Tr*). The coxal processes, however, would appear to have no particular function in connection with feeding. The dorsal surfaces of the coxae (E, *IICx*) are mostly membranous, but mesally where they join the epistome (*Epst*) each is strongly sclerotized in continuity with the upper surface of the anterior coxal process.

The telopodite of each pedipalp (fig. 7 B, *Pdp*) includes five thick, cylindrical, hairy segments, and an eversible adhesive end organ (*Ptar*). The end organ is an invaginated sack eversible from between two outer, hairless lips, the structure and mechanism of which has been fully described by Sørensen (1914), by Barrows (1925), and by Kästner (1933b). With each organ are associated the tendons of two muscles, one attached on the inner end of the sack, the other on the lower lip of the outer opening. The everted sack, supposedly forced out by blood pressure, assumes the shape of a stalked, cuplike pad; the muscles effect its retraction. These end organs of the pedipalps are evidently the pretarsi, the sacks being probably, as Sørensen says, the homologues of the plantulae, or empodia, of the walking legs. The everted pads are said to be adhesive organs which enable the solpugids to climb on smooth vertical surfaces, and Heymons (1901) asserts that they are used also for catching small insects, which adhere to their exposed surfaces.

Between the dorsal surfaces of the pedipalp coxae is a large, strongly convex epistomo-labral plate (fig. 7 E, *Epst, Lm*), the labral part of which projects as a free lobe between the divergent coxal processes (*cxp*). The labrum of the solpugid is not separated from the unusually long epistome (E, F), and some writers have regarded the whole plate as the labrum. However, since the proximal part of the plate (*Epst*) is united laterally with the mesal sclerites in the dorsal walls of the pedipalp coxae (E, *IICx*), and gives origin to the dilator muscles of the pharynx (G, I, *dld, dll*), this part has the distinctive features of an epistomal plate. Along the lines of union with the coxal sclerites (E, F, *ccs*) are inflected a pair of large, plate-like epistomo-coxal apodemes (E, F, *ccAp*) that extend proximal to the base of the epistome.

The relatively small labrum (fig. 7 E, *Lm*) projects as a free lobe from the end of the epistome, and conceals the mouth below its base (G). On its under surface the labrum bears two large, flat, closely adjacent brushes of long thick hairs beset with many small, delicate barbules, and united by transverse bars (F, G, H), so that each brush forms a fine-meshed sieve. Since these labral brushes guard the mouth behind them (H, *Mth*), they appear to constitute a filtering

apparatus for straining out particles of food too large to be swallowed.

The mouth of the solpugid (fig. 7 H, *Mth*) lies above the edge of a membranous ventral area in front of the tapering anterior end of the narrow deutosternum (*IIS*). Diverging at the sides of the mouth from this membranous area is a pair of large, flat, soft lobes (*ml*) with long apical setae, and each lobe bears a slender, finely hairy flagellum. These mouth lobes are characteristic features of the solpugids. Laterally each lobe lies adjacent to the free margin of the epistomal plate (*F*). The two mouth lobes, together with the labrum and the setal brushes, guard the entrance to the mouth, but they can hardly be said to form a preoral cavity. The gutterlike deutosternum (*B*, *H*, *I*, *IIS*) is deeply buried between the mesal surfaces of the pedipalp coxae (*I*, *IICx*), and its tapering anterior end (*H*) runs out into a shallow median groove that goes forward to the lower margin of the mouth. Possibly this sternal channel also has something to do with the oral conduction of food liquids.

The unusually large size of the epistomo-labral plate of the solpugids gave the earlier writers on these arachnids the idea that the solpugid mouth parts constitute a "beak." Bernard (1895), for example, says, "the beak is a marked feature of the Galeodidae"; he contended, furthermore, that a beak is a primitive arachnid structure, best preserved in the Solpugida, but variously reduced in the higher orders. Börner (1902) refers to the Solpugida and the Palpigradi as the only arachnids in which the mouth opening is situated on a cone, or so-called rostrum. What these writers call a beak, Police (1928) terms the "bucco-pharyngeal apparatus." The present writer sees no reason for regarding the mouth-bearing part of the solpugid as a "beak" or "rostrum" in any true sense. Only the labrum projects as a free lobe dorsally, with the mouth beneath its base as in other arachnids, and the ventral mouth lobes are special features of the solpugids. Police (1928) contends that the mouth lobes of the solpugids are homologues of the lobes of the pedipalp coxae in Phalangida and Araneida, which interpretation he says follows from Heymons' (1905) observation on their development. Heymons, however, says merely that the lobes develop mesad of the coxal processes of the pedipalps; there is little to suggest that they have any homology with coxal lobes of other arachnids.

The pharynx of the solpugids is an elongate sack (fig. 7 G, *Phy*) with soft walls devoid of sclerotic plates. In cross section it is triangular, but the walls are inflected between the angles, forming a three-pointed star (*I*, *Phy*). Posteriorly the lower lobe becomes much longer than the upper lobes (*D*). Dorsal dilator muscles of the

pharynx arise along the entire length of the epistome (*G, dld*); lateral dilators arise anteriorly on the epistome (*I, dll*), but posteriorly they spread to the epistomo-coxal apodemes. Constrictor fibers attached on the three pharyngeal ridges (*D*) alternate with the dilator fibers.

The solpugids are known to be voracious feeders on all kinds of insects, and it is well attested that larger species will attack, kill, and devour small vertebrates. It is recorded by Hutton (1843) that an Indian species of *Galeodes*  $2\frac{1}{2}$  to  $2\frac{3}{4}$  inches long kills and eats small lizards; Heymons (1901) says of *Galeodes caspius* that this species in captivity will eat small toads and lizards 2 to 3 cm. in length, and that a female in the open was seen feeding on a snake that had been killed by a railway train. The huge chelicerae are able to crush even the hardest beetles. In the case of large prey, Heymons observes, the solpugid first bites a hole in the body, and then tears out the soft inner parts until there is nothing left but the empty body wall. Smaller and weaker insects are directly chewed to a pulp in the chelicerae and the hard parts discarded. The fluid extracted from the prey presumably flows down between the chelicerae to the labrum, where it is filtered through the sieve brushes to keep large particles from reaching the mouth. The food is not known to be subjected to extraoral digestion.

The solpugids have often been accused of being venomous, but the chelicerae contain no poison glands, and the bite of a solpugid has been shown experimentally to be nonpoisonous, though admittedly the chelicerae might carry infective matter.

#### IV. THE PEDIPALPIDA

The name of this order is derived evidently from the fact that the "first legs" are long, slender, palplike appendages, in some forms so attenuated as to be almost filamentous, and have a sensory function. The so-called pedipalps, on the other hand, are strong prehensile organs and may be chelate. In one of the two principal groups of the pedipalpids, the Amblyphygi, the abdomen is broad and rounded; in the other, the Uropygi, it is more elongate and bears a caudal flagellum, which is either short (*Schizopeltidia*), or long and multiarticulate (*Holopeltidia*). The mouth parts are characteristically different in the two major groups.

With respect to the feeding organs the Amblyphygi are distinctly more generalized than the Uropygi. In each group the pedipalp coxae are extended forward far beyond the mouth; in the Uropygi they are united to form a preoral food trough, in the Amblyphygi

they are free from each other except at their bases (fig. 8 A, *IICx*) and the distal ends form a pair of large hairy processes (*cxp*). The labrum of the Amblypygi is a very small lobe overhanging the mouth (A, B, *Lm*). There is no distinct epistome, but a large, median epistomal apodeme is present (B, *eAp*) between a pair of lateral apodemes produced from the bases of the pedipalp coxae (A, B, *cAp*). The oral aperture beneath the labrum (B, *Mth*) opens directly into a simple, tubular pharynx (*Phy*), which in cross section is triangular and resembles the pharynx of the Solpugida. Dorsal dilator muscles of the pharynx arise on the epistomal apodeme, lateral dilators take their origins on the coxal apodemes (A, *Phy*). Because of the independence of the pedipalp coxae, and the small size of the labrum,

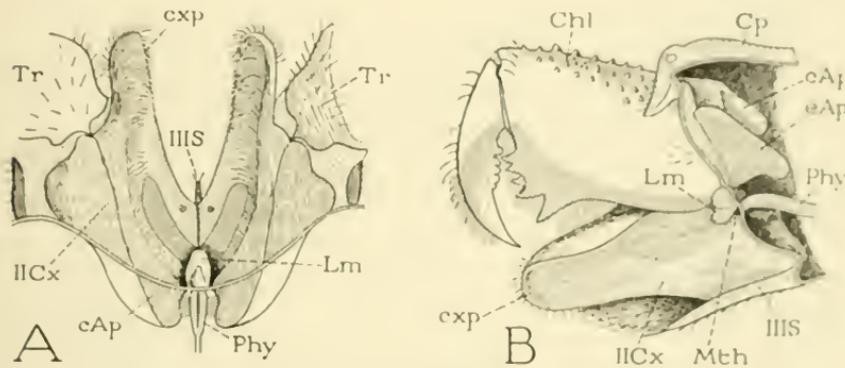


FIG. 8.—Pedipalpa-Amblypygi.

A, *Titanodamon johnstoni* (Poc.), Phrynidae, showing separation of pedipalp coxae, well-developed coxal processes (*cxp*), relatively small labrum (*Lm*), and simple pharynx (*Phy*) (from Pocock, 1902). B, *Phrynichus bacillifer* (Gerst), Phrynidae, longitudinal section through anterior end of body a little to left of median plane (from Börner, 1904).

the Amblypygi have no distinct preoral food cavity; the Uropygi, on the other hand, have a highly specialized prepharyngeal food passage between the large, thick labrum above and the trough of the united pedipalp coxae below.

The Uropygi include the "whip-tailed scorpions" (Thelyphonidae), well known from the East Indian *Thelyphonus* and the American *Mastigoproctus*. The following description of the mouth parts is based on *M. giganteus* (H. Lucas) of the southern United States.

The membranous anterior wall of the body of *Mastigoproctus* is set far back under a long, overhanging part of the carapace, the lower surface of which is strongly sclerotic and bears a median keel. Beneath this projection of the carapace, at the sides of the keel, arise the relatively short, two-segmented chelicera, the movable fingers of which

are dorsal in the Pedipalpida (figs. 8 B, 9 C). Below the chelicerae is a broad horizontal surface formed of a median epistomal plate (fig. 9 B, *Epst*) flanked by the large dorsal plates of the pedipalp coxae (*dplcx*). The epistomal plate is divided by a median groove, and from its end projects the elongate, tapering, hairy labrum (*Lm*) between the setigerous mesal surfaces of the anterior processes of the pedipalp coxae (*cxp*). At the base of the epistome there extends into the body cavity a strong apodemal arm (B, D, *eAp*), which, as shown by its muscle connections, is clearly the epistomal apodeme of other arachnids, though in the Thelyphonidae, as noted also by Pocock (1902), it is not connected with the base of the epistomal plate ("clypeus" of Pocock), but arises from the body wall just above the epistome.

The pedipalp coxae present ventrally broad, flat surfaces (fig. 9 A, *IICx*) in contact with each other for most of their length, there being no evident remnant of the deutosternum between them. Anteriorly, however, the coxae are produced into a pair of thick, widely divergent, triangular processes projecting mesad of the trochanters. The dorsal surface of each coxa, as above noted, contains a large plate (B, *dplcx*) united mesally with the epistome, and continuous anteriorly into the coxal lobe (*cxp*). Laterally the coxal plate bears the dorsal articulation of the trochanter (*Tr*), but behind the trochanter it is separated from the sclerotic lateroventral coxal wall by a membranous gap, and its posterior mesal angle is produced into a tapering apodemal process (B, D, E, *cAp*). The united parts of the pedipalp coxae of *Mastigoproctus* extend beyond the tip of the labrum (B), and form under the latter a deep trough (*PrC*), the lateral walls of which are membranous and densely clothed with hairs converging downward beneath the labrum. The cavity thus enclosed is the anterior, open part of a preoral food passage leading back to the sucking organ. The posterior part of this passage has a highly specialized type of structure not known in any other group of arachnids.

The ingestion apparatus of the Thelyphonidae has been described by several writers, including Bernard (1893), Börner (1901, 1904), and Kästner (1932a), but it is most clearly portrayed by Pocock (1902). At the inner end of the open cavity between the labrum and the trough of the united pedipalp coxae is a semicircular slit concave dorsally. From this slit there continues posteriorly a semi-cylindrical crevice-like passage (fig. 9 G, *PrC*) between a ventrally convex dorsal plate, or *lamina dorsalis* (*lmd*), and a dorsally concave ventral plate, or *lamina ventralis* (*lmv*). The dorsal plate is the under wall of the labrum (*Lm*), the ventral plate is a continuation from

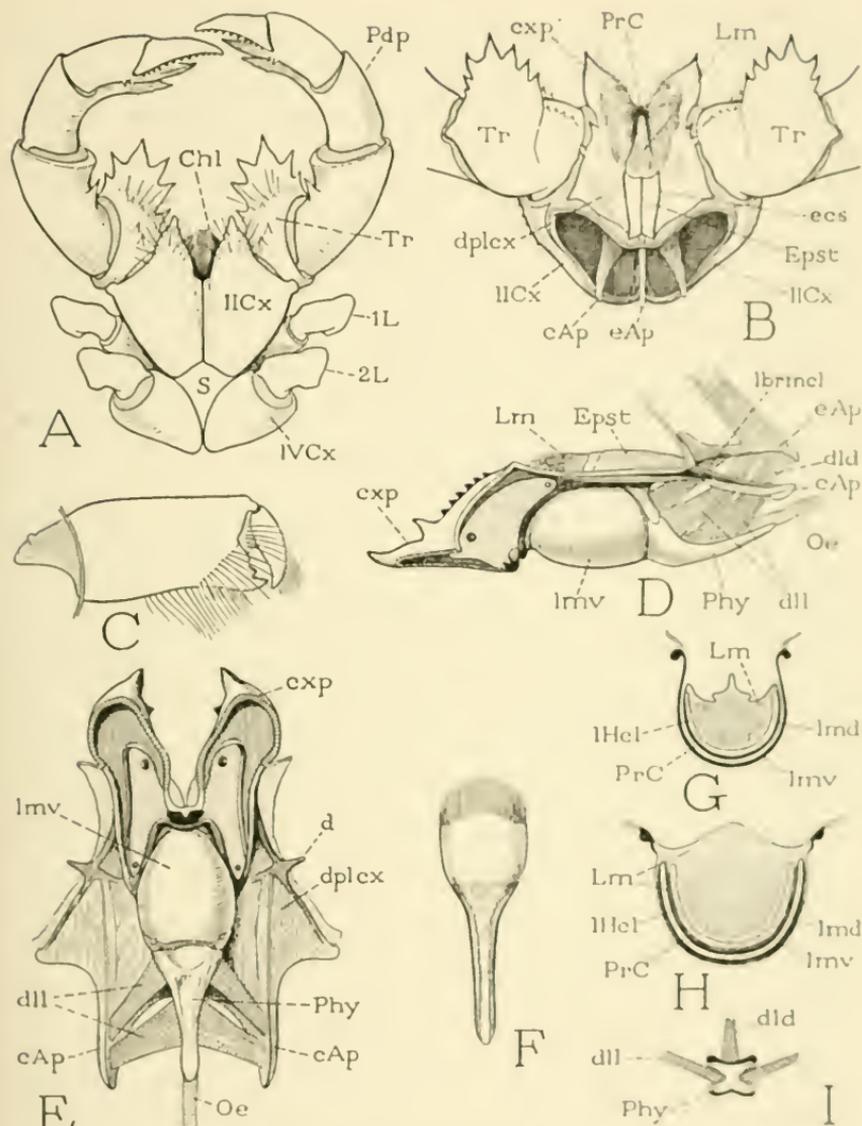


FIG. 9.—Pedipalpida-Uropygi-Thelyphonidae, *Mastigoproctus nauticus* (H. Lucas).

A, anterior part of body, with pedipalps and bases of first two pairs of legs, ventral. B, mouth region, dorsal, as seen by removal of chelicerae. C, chelicera. D, lower wall of preoral cavity and pharynx, with muscles of labrum and pharynx, exposed by removal of left side of left pedipalp coxa. E, ventral walls of pedipalp coxae removed, exposing dorsal coxal walls, and ventral walls of preoral cavity and pharynx, with pharyngeal muscles. F, lamina dorsalis of preoral cavity and pharynx. G, cross section through anterior part of labrum and preoral cavity. H, section through middle of labrum and preoral cavity. I, section of pharynx.

the floor of the trough of the united coxae. The dorsal wall of the labrum (*Lm*) is a mass of spongy but dense tissue, so thick that it reduces the haemocoel of the labrum to a narrow slit (*lHcl*) concentric with the lumen of the food passage (*PrC*) below it. Pocock (1902) says the cavity of the labrum ("camarastome") "is filled for the most part with muscles which pass from its roof to its floor," but he evidently was mistaken as to the nature of the tissue in the labrum, and he must have missed the narrow haemocoel in its lower part. An anterior bundle of muscle fibers from the epistomal apodeme (*D, lbrmcl*), however, does attach to the posterior end of the thick dorsal wall of the labrum and merges into its spongy tissue. Behind the base of the labrum, the lamina dorsalis and the lamina ventralis are united along their upper edges (*H*), so that the food passage between them (*PrC*) becomes a closed cavity.

When this structure is seen from the side (fig. 9 D) or from below (*E*), the lamina ventralis of the food passage appears as a large, strongly convex, ovate body (*lmv*) firmly suspended from the median edges of the dorsal plates of the pedipalp coxae (*E, dplcx*). The wide posterior end of the lamina ventralis narrows into a long, free, tapering arm (*Phy*), which is the ventral wall of the sucking part of the ingestion apparatus, and is therefore the ventral plate of the pharynx. The lamina dorsalis (*F*) has a form similar to that of the lamina ventralis upon which it is closely superposed. Its anterior margin bears a fringe of long hairs guarding the slitlike opening of the food passage above mentioned; its posterior part tapers into the dorsal plate of the pharynx. The two plates of the pharyngeal region are connected by infolded lateral membranes (*I*) allowing of expansion and contraction. Dorsal dilator muscles of the pharynx (*D, I, dld*) arise on the epistomal apodeme (*D, eAp*); lateral dilators (*dll*) arise on the basal apodemes of the pedipalp coxae (*D, E, cAp*). Inasmuch as the pharyngeal plates of *Mastigoproctus* are directly continuous from the dorsal and ventral plates of the prepharyngeal food passage, the so-called pharynx is differentiated from the latter only by its expansible lumen and the possession of dilator muscles.

No functional explanation can readily be given for this curious ingestion apparatus of the Thelyphonidae. In a preserved specimen the dorsal and ventral plates of the prepharyngeal section are in close apposition, and there appears to be here no mechanism for expansion. Certainly nothing but liquid could be sucked through the passage, and the fringe of hairs at the entrance on the lamina dorsalis must effectively keep out food particles. The thelyphonids feed on insects and other terrestrial arthropods. They are said to seize and crush their

prey with the pedipalp chelae, and to further lacerate it with the chelicerae. The exuding juices, caught in the open trough of the pedipalp coxae, must be sucked in by the action of the pharynx. No evidence of extraoral digestion by these arachnids has been observed.

#### V. THE RICINULEI

The small and rare arachnids of this order include 12 known living species from Africa, Central America, and South America, and extinct Palaeozoic species from Europe and North America. The living forms, according to Ewing (1929), belong to two genera: one, *Ricinoides* Ewing (formerly *Cryptostemma*) is represented by six species in Africa, the other, *Cryptocellus* Westwood, includes six American species. The structure of the feeding organs of the Ricinulei is known only from the work of Hansen and Sørensen (1904), the scarcity of specimens in collections making them too valuable for anatomical purposes.

A distinctive feature of the Ricinulei is the presence of a large hoodlike lobe, the *cucullus*, movably hinged to the anterior margin of the carapace, which ordinarily (fig. 10 B, *Cuc*) conceals the chelicerae and the mouth region below it (*A*). The under surface of the cucullus bears a median ridge separating lateral concavities that fit over the chelicerae, which structure, as noted by Hansen and Sørensen (1904), suggests that the ricinuleid cucullus represents the anterior part of the carapace of the Thelyphonidae that overhangs and conceals the chelicerae. The chelicerae of the Ricinulei (*D*) are two-segmented as in the Pedipalpida. The small, chelate pedipalps (*A*, *B*, *Pdp*) have a ventral position, and their coxae are completely united to form a trough below the mouth. The pedipalp segmentation (*E*) is simple compared with that of the legs (*B*), there being two trochanteral segments (*1Tr*, *2Tr*) as in the legs, but the tibia is a long slender segment (*Tb*), and the tarsus (*Tar*) forms the small movable finger of the chela. In the legs (*B*) a patella intervenes between the femur and the short tibia, while the tarsus is divided into a long basal subsegment and five short distal subsegments.

The mouth region of the Ricinulei (fig. 10 C) resembles that of the Thelyphonidae (fig. 9 B) in that the floor of the preoral cavity (*PrC*) is formed by the united pedipalp coxae. In the ricinuleid, however, there are no free coxal processes since the coxae are here entirely united in a broad, troughlike under lip (fig. 10 C, *Hst*), which would appear to be quite comparable to the hypostome of Acarina (fig. 26 A, B, *Hst*). Projecting over the proximal part of the

coxal trough is the rounded labrum (*C, Lm*), which is supported on a large epistomal plate (*Epst*) united laterally with the dorsal walls of the adjoining parts of the pedipalp coxae. The epistome and the labrum together are regarded by Hansen and Sørensen as "pars basalis" and "pars apicalis" of the labrum, but these writers note the

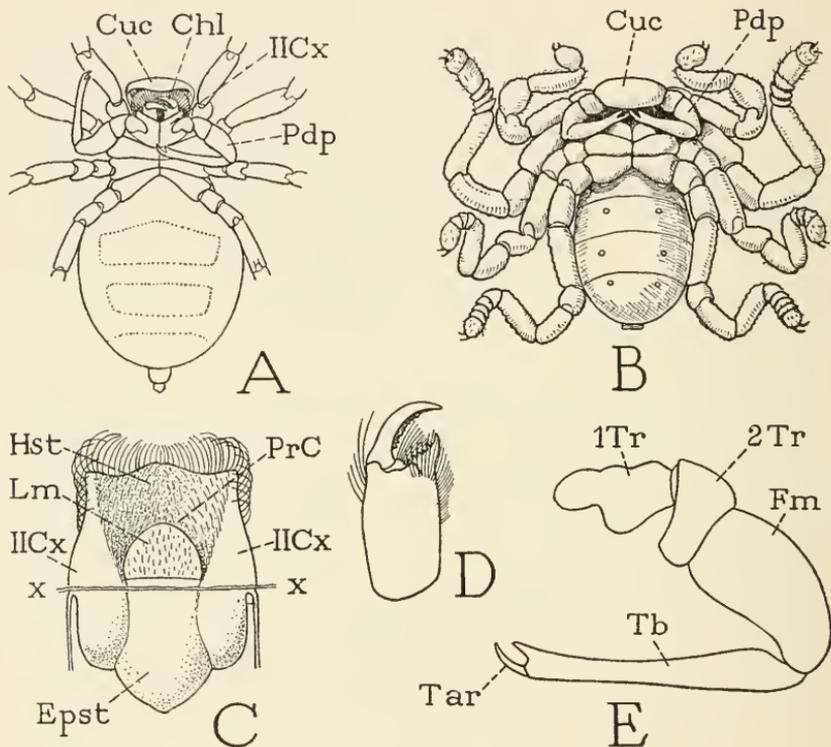


FIG. 10.—Ricinulei.

A, *Ricinoides crassipalpe* (H. & S.), ventral, with cucullus (*Cuc*) turned forward exposing the chelicerae (outline from Hansen and Sørensen, 1904). B, *R. westermanni* (Guérin), cucullus closed over labrum and chelicerae (from Karsch, 1893). C, *R. crassipalpe* (H. & S.), mouth region, dorsal, showing pedipalp coxae completely united in a broad under lip (*Hst*); *x-x*, line of invagination of basal parts of coxae and epistome (from Hansen and Sørensen, 1904). D, *R. karschii* (H. & S.), chelicera (from Hansen and Sørensen, 1904). E, *R. sjöstedtii* (H. & S.), segmentation of the pedipalp (outline from Hansen and Sørensen, 1904).

distinctive features of the two parts, and that the "pars basalis" gives attachment to the dilator muscles of the sucking pump. The basal parts of the coxae and the greater part of the epistome are said to be invaginated into the body cavity proximal to the line *x-x* of the figure.

The internal part of the ingestion apparatus of the Ricinulei is not

fully or clearly described by Hansen and Sørensen from the single specimen at their disposal. A transverse "crest," concave dorsally, is said to be suspended from the united pedipalp coxae ("mandibles") and epistome, which is perforated by the oesophagus. From this we may suspect that there is here a structure resembling that in the Thelyphonidae. Muscles of the oesophagus and pharynx, according to Hansen and Sørensen, arise on the epistome ("pars basalis"), and also "muscles attached to the base of the pars apicalis." The last suggest the epistomal muscles inserted into the base of the labrum in *Mastigoproctus* (fig. 9 D, *lbrmcl*).

## VI. THE CHELONETHIDA, OR PSEUDOSCORPIONIDA

The external anatomy of the pseudoscorpions, together with the respiratory system and the reproductive organs, has been described in great detail by Chamberlin (1931), and full accounts of the external and internal structure are given in the comprehensive works of Kästner (1927), Beier (1932), and Roewer (1936). The structure of the chelonethid feeding apparatus was correctly known to Croneberg (1888), and the external mouth parts are well portrayed by Pocock (1902). The information here given is taken mostly from these sources.

The conspicuous feature of the pseudoscorpions is the great relative size of the chelate pedipalps (fig. 11 A). The chelicerae (*Chl*) are small, two-segmented, and project straight forward from beneath the edge of the carapace. Below the chelicerae is a group of structures that constitute the mouth parts, including the labrum (*Lm*) above, a narrow under lip (*lpg*) below, and anterior processes of the pedipalp coxae (*IICx*) on the sides. The coxae of the pedipalps, as those of the legs, are almost contiguous along the midventral line of the body, being separated only by a narrow membranous space in which are no remnants of segmental sternal plates. The coxae themselves thus replace the sterna and become the actual ventral exoskeleton of the prosoma.

The chelonethid chelicerae (fig. 11 B, E) have an unusually elaborate structure, because, as Chamberlin (1931) points out, they are used for several specific purposes besides that of holding the prey during feeding. The pincers serve for carrying sand grains or other material used in nest-building, the movable finger gives exit to a silk-producing gland, and bears usually a spinneret near its apex; the chelicerae, furthermore, serve as cleaning organs, in adaptation to which function the fingers are equipped with membranous folds,

called *serrulae*, and finally they are the seat of important sense organs. The serrulae have different forms in different species (fig. 11 B, E, *Ser*), but characteristically the structures so called are thin folds or more or less free appendages either indented along the outer margin (C, *Ser*), or incised to form a comblike organ (E). The

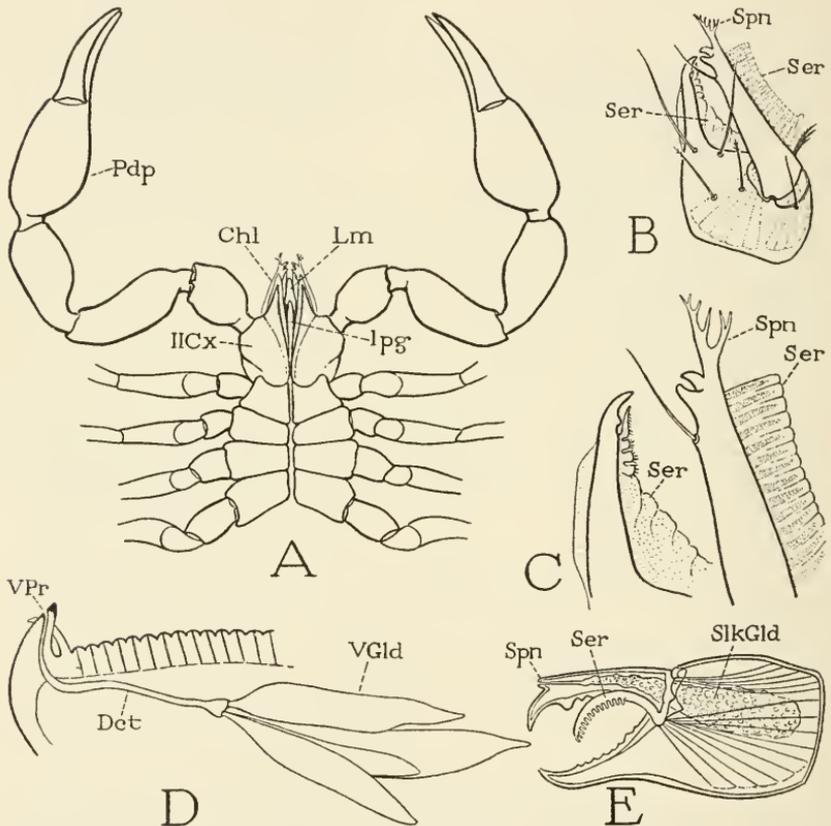


FIG. 11.—Chelonethida.

A, a pseudoscorpion (probably *Chelanops* sp.), female, prosoma and appendages, ventral. B, same, right chela, dorsal. C, same, details of cheliceral fingers, more enlarged. D, *Atemnus* sp., venom glands of pedipalp chela, with duct opening near apex of movable finger (from Chamberlin, 1931). E, *Chthonius* sp., chelicera, showing silk gland with duct opening through spinneret on movable finger (from Barrows, 1925).

cheliceral silk gland, shown contained within the chelicera at E of figure 11 (*SlkGld*), generally extends into the body cavity. There may be a single duct opening through a simple papilliform spinneret on the convex side of the movable finger (E, *Spn*), or there may be several ducts opening separately through the prongs of a branched

spinneret (B, C, *Spn*) known as the "galea." The spun silk is used for the making of cocoonlike nests in which the animal encloses itself for moulting, brood purposes, or for hibernation. The silk glands, therefore, are best developed in the immature stages and in the adult female; the glands of the adult male become reduced, and in some cases they appear to be absent.

The female pseudoscorpion deposits her eggs in a gelatinous brood sack attached around the genital aperture on the under side of the abdomen, and the young after hatching undergo their development here, fed on an albuminous substance discharged from the ovaries of the mother, until they are fully formed young pseudoscorpions. Some species carry the eggs and the young about with them in the open, but with most species the female encloses herself in a silken cocoon until the young are able to live independently. The remarkable metamorphosis that the young pseudoscorpion undergoes during its development is described by Barrois (1896), and an interesting account of the construction of the brood cocoon is given by Kew (1914).

The chela of the chelonethid pedipalp, as already shown (p. 14, fig. 5 G), has the same general structure as the chela of a scorpion (fig. 5 E, F) but it possesses the unique feature of containing in most species one or two glands supposed to secrete a venomous liquid. According to Chamberlin the glands may be present in both the movable and the fixed finger, in the movable finger only, or in the fixed finger only; in four families, however, they are absent. Each gland (fig. 11 D, *VGld*) consists of several elongate sacks with a common duct (*Dct*) opening through a pore (*I'Pr*) on a subapical, toothlike process on the convex side of the finger containing the gland.

The coxae of the pedipalps are free from each other, and are connected only at their bases with the narrow membranous ventral wall of the body between them (fig. 12 B, *IICx*). Anteriorly the coxae are produced into a pair of thick processes (*c.rp*), normally embracing the labrum (figs. 11 A, 12 A). Though these coxal extensions are called "manducatory" processes, they have no chewing function, and serve merely to form the lateral walls of the preoral food chamber. A flat dorsal appendage arising from the base of each lobe in most species, and a thin ventral flange (fig. 12 A, *ls, li*) are known respectively as the *lamina superior* and the *lamina inferior*.

The labrum projects between the coxal processes of the pedipalps as a free lobe of varying width in different species (fig. 12 A, B, *Lm*). The dorsal surface of the labrum is continued proximally into an epistomal plate (A, *Epst*), which is mostly invaginated into the anterior body wall below the bases of the chelicerae, and thus becomes prac-

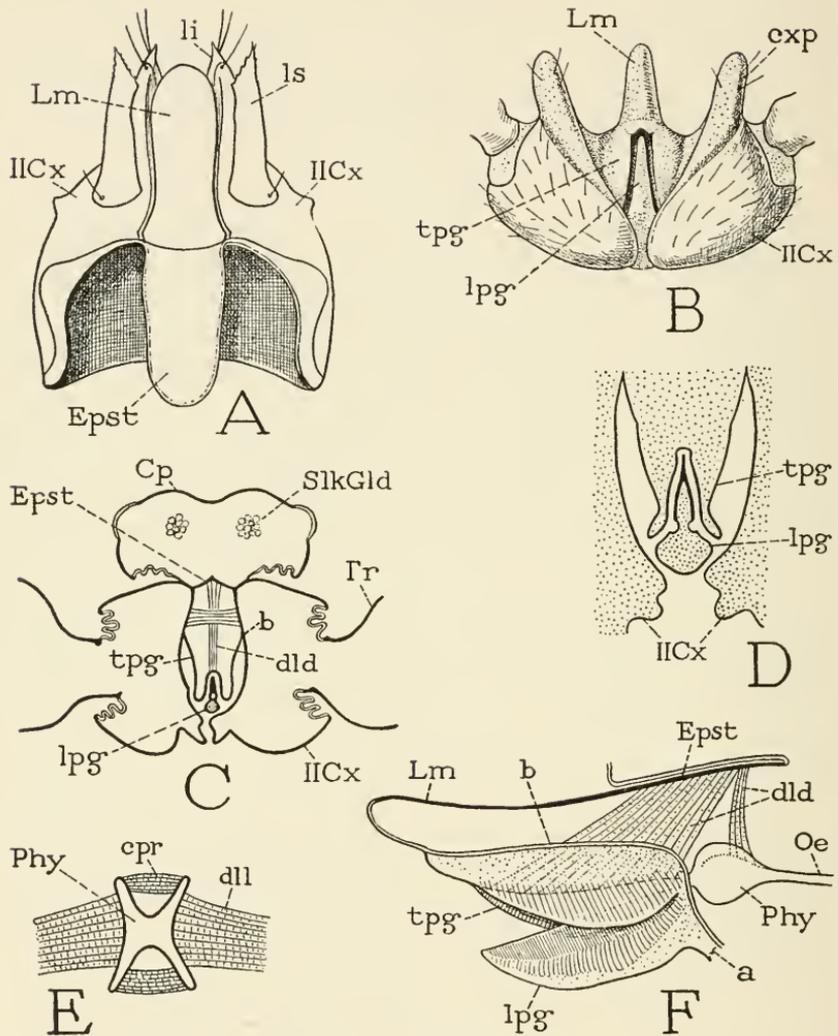


FIG. 12.—Chelonethida.

A, *Apochthonius intermedius* Chamb., mouth parts, dorsal; *li*, *ls*, appendicular lobes of pedipalp coxae (from Chamberlin, 1931). B, *Garypus* sp., mouth parts, ventral, pedipalp coxae spread apart showing lophognath (*lpg*) in groove of taphrognath (*tpg*) (from Pocock, 1902). C, *Garypus sini* Chamb., cross section through anterior part of carapace and bases of pedipalps, showing relation of lophognath (*lpg*) to taphrognath (*tpg*) (from Chamberlin, 1931). D, same, section of taphrognath and lophognath more enlarged. E, same, cross section of pharynx (from Chamberlin, 1931). F, diagram of chelonethid ingestion apparatus based on Croneberg (1888) and Chamberlin (1931); *a*, connection of lophognath with pedipalp coxa, *b*, cut edge along *b* in C.

tically an apodemal structure. The chelonethid epistome is termed by Chamberlin the "intermaxillary jugum" because its distal part is united with the pedipalp coxae, which are commonly called "maxillae"; but on its under surface are attached the usual dorsal muscles of the ingestion apparatus (F), showing that the plate in question is that here termed the epistome in other arachnids. The epistome is similarly invaginated or overgrown in the Ricinulei and some Acarina, and in the last order is known as the "subchelicerai plate."

The under surface of the labrum is continued posteriorly as the dorsal wall of the preoral food passage, and is produced into an elongate lobe (fig. 12 B, *tpg*) enclosed between the mesal surfaces of the pedipalp coxae (which latter, as shown at B, are spread apart). The under surface of the lobe is deeply channeled lengthwise, and receives the narrow under lip (*lpg*), which carries a high, crestlike ridge on its upper surface, as seen in cross section at D. Chamberlin (1931) likens these two structures to a pair of jaws lying one above the other. The upper grooved "jaw" he terms the *taphrognath*, the lower crested "jaw" the *lophognath*.

The so-called lophognath, or under lip, is a laterally compressed, tapering, median lobe projecting forward from the venter of the prosoma between the bases of the pedipalp coxae (fig. 12 B, *lpg*), and would thus appear to be a sternal structure, as said by Pocock (1902). Chamberlin shows that the lophognath is attached by two basal arms to the pedipalp coxae, but its form and structure do not suggest that the lophognath itself is of coxal origin.

The relation of the taphrognath and the lophognath to each other is shown diagrammatically at F of figure 12, in which the lophognath (*lpg*) is partly exposed by being pulled down from the groove of the taphrognath (*tpg*). The opposing surfaces of the taphrognath and the lophognath are shown by Chamberlin to be corrugated by numerous fine, closely set, transverse ridges, fringed with minute spines directed inward. The exposed lateral surfaces of the two lobes are also ridged, but on these areas the ridges are somewhat farther apart. On the crest of the taphrognath are inserted the fibers of a large flat muscle (C, F, *dld*) having its origin on the under surface of the invaginated epistome (*Epst*).

At their inner ends the taphrognath and the lophognath are united by a union of the lips of the former with the sides of the latter (fig. 12 F). There is thus formed here the true oral aperture, which opens immediately into a relatively small, pear-shaped pharyngeal sack (*Phy*). This organ shows in cross section (E) the usual structure of the arachnid pharynx; the concave dorsal, ventral, and lateral walls

give a four-rayed figure. Constrictor muscles attached on the points of the folds are shown by Croneberg (1888) to surround the pharynx; lateral constrictor muscles are said to be present by Chamberlin (1931), though they are not shown in his figure (E). Lateral dilator muscles (*dll*) inserted on the side walls of the pharynx have their origins on the lateral walls of the pedipalp coxae. Chamberlin makes no mention of dorsal dilators, but Croneberg specifically says that a group of fibers from the epistome ("basal part of the rostrum") goes to the pharynx, as is shown in the diagram at F. The distribution of most of the epistomal muscles on the preoral under surface of the labrum is an unusual condition found only in the Chelonethida, but it can be correlated with that in the Solpugida, in which a few of the anterior fibers extend into the labrum (fig. 7 G), and is suggestive of that in *Mastigoproctus* in which a large bundle of epistomal fibers goes to the posterior end of the labrum (fig. 9 D, *lbrmcl*).

The chelonethid ingestion apparatus has no duplicate among other arachnids, and no other even approaches it in structure. The taphrognath might be likened to the lamina dorsalis of the food passage in Thelyphonidae, but the lophognath is not comparable to the lamina ventralis, and the sacklike chelonethid pharynx is quite distinct from the preoral part of the feeding apparatus. The principal sucking organ of the chelonethids would appear to be the preoral structure formed of the taphrognath and the lophognath, rather than the relatively small pharynx. A lifting of the taphrognath from the lophognath by a contraction of its dorsal muscles (fig. 12 F) would draw the liquid food into the taphrognathic channel, where, by a reversal of the action, it would be impelled back to the mouth to be sucked into the pharynx. The food-conducting channel from the prey, however, as Chamberlin notes, must be formed by the approximated laminae of the pedipalp coxae and the distal part of the labrum (A).

The Chelonethida are said to catch and kill their victims with the pedipalp chelae, from which the prey is given to the chelicerae to be held while feeding. Chamberlin (1931), in describing the feeding of *Chelifer fuscipes* Banks on a small lepidopterous larva, says the active caterpillar, grasped and tightly held in the chela, becomes motionless in 30 seconds, and is then drawn up to the mouth parts and seized by the chelicerae. In a few minutes the larva becomes much shrunken, when a new hold is taken by the chelicerae and feeding resumed at another point of attack. Schlottke (1933b), observing the feeding of *Chelifer cancroides* L. on meal worms, notes that the sucking of the larval juices is preceded by an inflation of the larva with a secretion from the mouth of the chelonethid, which evidently liquefies the

tissues of the prey. During feeding the soft-skinned larva thus alternately expands and contracts according to whether it is being injected with the solvent liquid or exhausted by suction. Though *Chelifera* is classed by Chamberlin as a genus having a venom gland in each finger of the chelae, Schlotzke says no poisonous effect was to be observed on the captured prey.

## VII. THE SCORPIONIDA

With the scorpions more parts of the animal's anatomy have been brought into the service of the feeding function than in any other arachnid. There is present the usual association of the chelicerae, the labrum, and the pedipalp coxae, but the under lip of the scorpion is composed of endite lobes from the coxae of both the first and the second pairs of legs, the pedipalps bear strong chelae, and, in addition to these structures, the postabdominal tail with its sting plays an important role in the feeding process by the subduing of prey caught and held in the pedipalp chelae.

The relatively small, three-segmented chelicerae of the scorpion project straight forward from beneath the overhanging edge of the carapace (fig. 13 A). They are turned on their sides so that the movable finger of each appendage has a lateral position. In *Centruroides* this finger is deeply cleft into two points (B, C), which clasp the immovable finger when the pincer is closed. The pedipalp chelae of the scorpion have been sufficiently described in the General Discussion (p. 14, fig. 5 D, E, F), in which the identity of the segments composing the chela was deduced from a comparison with the structure and musculature of the legs; the "hand" of the chela is the tibia, the movable finger is the tarsus, with possibly the tip derived from the pretarsus.

Conspicuous at the anterior end of the scorpion's body is a large, open, quadrate cavity (fig. 13 D, *PrC*) between the flat mesal surfaces of the pedipalp coxae (*IICx*), covered above by the flattened chelicerae (*Chl*), and closed below by the closely appressed endite lobes of the coxae of the first and second legs (*IIIEndt*, *IVEndt*). This cavity is evidently a receiving chamber for food material crushed by the pedipalp chelae and further comminuted by the chelicerae. Concealed within it is the labrum, and below the latter the mouth, both being fully exposed on removal of the chelicerae and the pedipalps (E). The labrum (*Lm*) is a large, soft, laterally compressed lobe with a rounded dorsal wall terminating in a fringe of long hairs (G, *Lm*), below which the anterior labral wall recedes to the short ventral

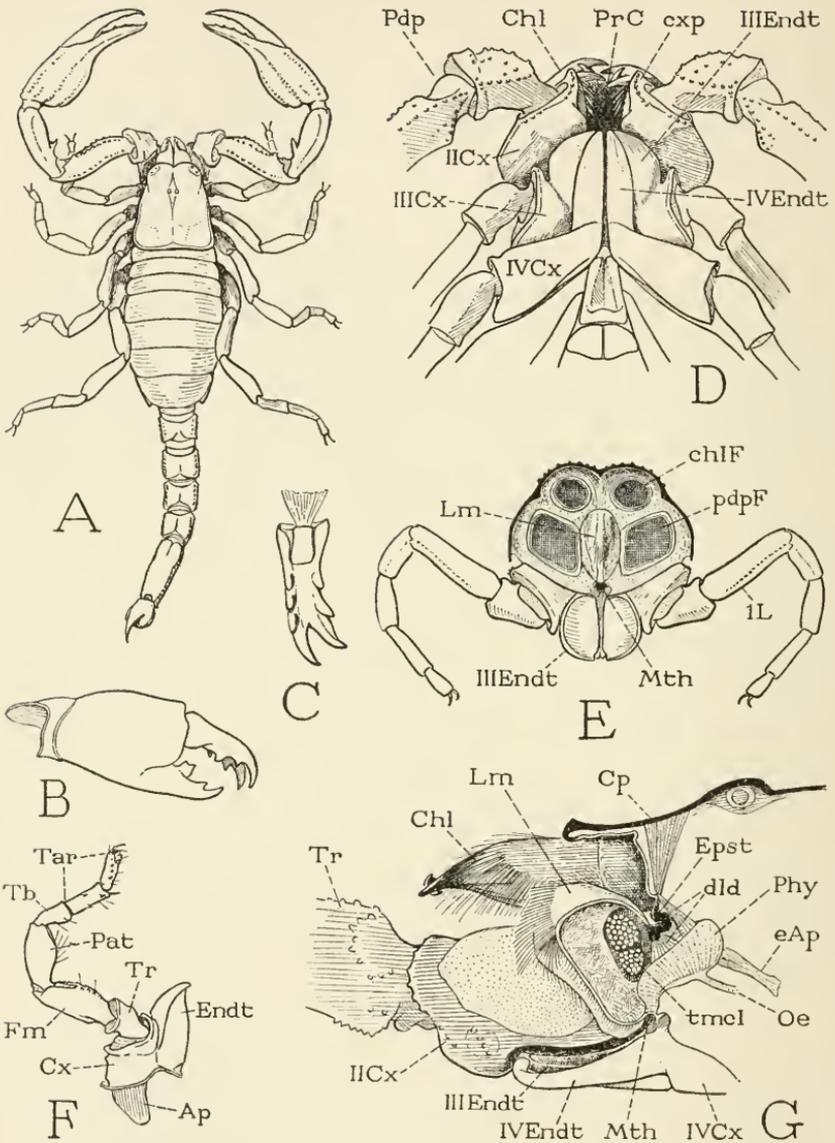


FIG. 13.—Scorpionida.

A, *Chactas vanbenedeni* Gervais, female. B, *Centruroides* sp., chelicera. C, same, movable finger of chelicera, mesal surface. D, same, anterior part of body, ventral, showing mouth parts and large preoral food cavity (PrC). E, same, anterior end of body with chelicerae and pedipalps removed, exposing the mouth (Mth) at base of coxal endites forming a basinlike under lip. F, *Pandinus* sp., right first leg, ventral, showing large coxal endite. G, *Centruroides* sp., longitudinal section through anterior end of body and labrum, with right chelicera and base of right pedipalp in place.

surface overhanging the mouth and the inner end of the preoral food cavity. The mouth (E, G, *Mth*) is a small unguarded aperture beneath the base of the labrum. From below the mouth there projects forward the broad, basinlike floor of the preoral cavity (E) formed of the endite lobes of the first leg coxae (*IIIEndt*). Between the mesal edges of these coxal lobes is a groove, which is closed below by the closely applied endites of the second leg coxae (D, *IVEndt*), and proximally runs into the mouth (E, *Mth*). The pedipalp coxae are entirely separated from each other, and there is no recognizable remnant of the pedipalp sternum in the scorpion. The broad, flat, mesal surfaces of the coxae are mostly membranous (G, *IICx*), and form the lateral walls of the preoral food cavity (D, *PrC*). Anteriorly the coxae are produced into short coxal processes (*cxp*) mesad of the trochanters. The coxal bases are connected by two thick bundles of transverse muscle fibers, which pass through the labrum (G, *tmcl*). These muscles occur in other arachnids, and are labral muscles; in the scorpion they appear to be operative on the pedipalp coxae by reason of a union of the base of the labrum with the coxal walls.

The lobes of the first and second leg coxae (fig. 13 D, *IIIEndt*, *IVEndt*) that form the lower lip of the scorpion, or floor of the preoral cavity, are here termed *endites* because they arise from the bases of the coxae (F) and not from their distal ends as do the coxal processes (*cxp*) of the pedipalp coxae. Coxal lobes of the same nature occur also in the Phalangida.

There is no prominent epistomal plate in the scorpion, but at the base of the dorsal wall of the labrum is a strong, irregular sclerotization (fig. 13 G, *Epst*), which clearly represents the epistome, since on it are attached the dorsal dilators of the pharynx (*dld*), and from it is given off a pair of apodemal arms (*cAp*).

The pharynx of the scorpion is a small, pear-shaped sack enlarging upward and posteriorly from its narrowed entrance at the mouth (fig. 13 G, *Phy*). It is somewhat compressed laterally, rounded at the inner end; the slender oesophagus (*Oe*) departs from the lower wall at the end of a ventral channel from the mouth. The dorsal wall of the sack is deeply infolded and the trough of the invagination is strengthened by an elastic rod. Dilator muscles attached on the concave dorsal wall (*dld*) arise on the epistomal sclerotization (*Epst*) at the base of the labrum, and lateral dilators take their origins on the epistomal apodemes (*cAp*). Compressor muscles cover the lateral walls of the pharynx.

The sting of the scorpion appears to be an appendage of the last

abdominal segment (fig. 14 B), and not the terminal segment itself. The end segment, or telson, of an arthropod contains the anus; in the scorpion the anus lies before the base of the sting in the end of the sting-supporting segment (A, *An*). The scorpion sting in its relation to the end of the abdomen is comparable with the flagellum of the Thelyphonidae and the tail spine of *Limulus*. The base of the sting is articulated on the end of the supporting segment in such a manner that its principal movement is in a vertical plane, but because

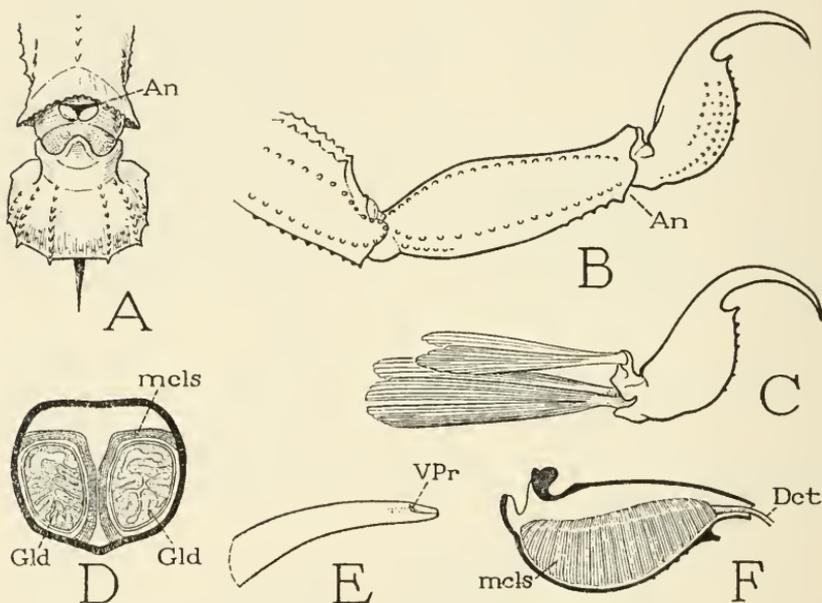


FIG. 14.—The sting of a scorpion.

A, *Pandinus* sp., end of last postabdominal segment, with the sting, ventral, showing the anus (*An*) in last segment at base of sting. B, *Centruroides* sp., last two postabdominal segments and the sting, lateral. C, same, the sting with its muscles arising in the last segment. D, same, cross section through base of sting, showing the venom glands and enclosing muscles. E, same, terminal part of sting, showing aperture of left venom duct. F, same, right half of base of sting, mesal view, showing muscles covering right gland, and duct.

of the amplitude of the articular membrane it is capable also of lateral movements. On its base are attached four long muscles, two dorsal, and one on each side (C). The dorsal muscles are widely divergent but both are inserted on a strong dorsal process of the sting base. The lateral muscles are attached below the articular points of the sting, and are hence depressors, but probably, acting as antagonists, they produce also lateral movements of the sting; each lateral muscle separates into two distinct bundles of fibers. The segments of

the postabdomen are likewise strongly muscled, each being provided with a single wide dorsal muscle with an axial tendon, a lateral muscle on each side, and in addition a large median ventral muscle.

The venom of the scorpion is produced in two sacklike glands contained within the swollen basal part of the sting (fig. 14 D, *Gld*). The glands have individual ducts opening separately near the point of the sting through two lateral pores (E, *l'Pr*), from which grooves extend to the tip. Each gland is closely invested along the entire length of its mesal and dorsal surfaces by a thick muscular sheath made up of several layers of semicircular fibers (D, F, *mcls*), attached dorsally on the upper part of the lateral wall of the containing capsule, and ventrally on the lower wall. Contraction of the muscles evidently compresses the gland sacks against the rigid capsular walls.

The scorpion is certainly not a primitive arachnid, though an ancient one. *If*, therefore, the scorpions have any relationship to the extinct Eurypterida, the theory of Versluys and Demoll (1920), insofar as it derives the eurypterids from primitive scorpions, would appear to be more reasonable than the reverse. That the Xiphosurida have a scorpion ancestry, however, is difficult to believe, considering their primitive method of feeding and their evident relation to the trilobites.

### VIII. THE PHALANGIDA, OR OPILIONES

The Phalangida are characterized by the presence of lobes arising from the *bases* of the coxae of the pedipalps and the first two pairs of legs. Because of their position on the coxal bases these lobes of the phalangiids are analogous to the lobes on the second and third leg coxae of the scorpions, which, as explained in the last section, are here termed *endites* to distinguish them from the distal processes of the pedipalp coxae in other arachnids. The pedipalp endites of the Phalangida are always closely associated with the mouth, and have the appearance of a pair of jaws; they may be prehensile, but they have no masticatory function, and hence are not appropriately termed "manducatory" lobes. The first leg endites in the Phalangiidae resemble the pedipalp endites and are likewise associated with the mouth, but the endites of the second legs never have a direct relation to feeding. In the Cyphophthalmi and the Laniatores the coxal endites, whether hard or soft in texture, are immovably fixed on the coxae, but in the Palpatores they are flexibly attached to the coxae, and become independently movable because some of the body muscles of the coxae are attached on their bases. A labrum is always present,

supported on an epistomal plate between the pedipalp coxae. An under lip, when present, is formed by the projecting sternum of the first-leg segment.

The mouth parts of the Cyphophthalmi, of which a general comparative account is given by Hansen and Sørensen (1904), are of more simple structure than those of the other two suborders of the Phalangida. The following description of the parts in *Holosiro acaroides* Ewing is made from specimens furnished by Dr. I. M. Newell of the University of Oregon.

The chelicerae of *Holosiro* (fig. 15 C) are relatively long, and are three-segmented, with the movable finger of the chela articulated laterally on the second segment. The pedipalp telopodites (I, *Pdp*) are slender, smaller than the legs, but the coxae (*IICx*) are large, and each bears a large endite (*IIEndt*) projecting ventrally and mesally. On removing the appendage, the endite is seen to be a solid extension from the inner face of the coxa (A, B, *Endt*) ending with a soft ventral lobe. The convex outer surface of the lobe (A) is clothed with small setae, the flat or slightly concave inner surface (B) is finely and closely striated. The two apposed pedipalp endites present ventrally rounded padlike surfaces (I, *IIEndt*) separated by a narrow cleft that leads up to the mouth. Though coxal muscles of the pedipalps are attached on the endites, the latter are so firmly fixed on the coxae that they have no independent movement.

The mouth of the Cyphophthalmids is entirely concealed beneath the bases of the chelicerae and between the pedipalp endites. Above the mouth is a U-shaped epistomal plate (fig. 15 D, *Epst*) supporting the labrum (*Lm*). In the specimens of *Holosiro* examined, the labrum was broken in dissection, but Hansen and Sørensen (1904) describe the organ in other cyphophthalmids as a thin, laterally compressed plate projecting downward and forward from the "clypeus" between the pedipalp coxae. The "clypeus" of these writers is the epistome.

The ventral surface of the prosoma of *Holosiro* (fig. 15 I) is occupied entirely by the large coxal segments of the legs, the long axes of which radiate on each side from a point in front of the genital opening. The coxae of the first legs (*IIICx*) are thus turned forward so that they embrace the pedipalp coxae (*IICx*). Each first-leg coxa is traversed anteroposteriorly across its middle by a strong ridge (*cxr*) that runs out in a small point on the anterior coxal margin, and forms the lower edge of a broad, slightly concave surface on the inner side of the coxa (E, F, I), which bears at its mesal end a soft, rounded, lobular endite (*Endt*) with a small, hairy papilla behind the pedipalp endite. Between the two opposed mesal surfaces of the first-leg coxae

is a widely open space, the so-called *stomotheca*, in which are contained the endites of the pedipalps and the first legs (I). Posteriorly the stomotheca is closed by the approximated inner ends of the second-leg coxae (*IVCx*), on which are rounded elevations of an endite

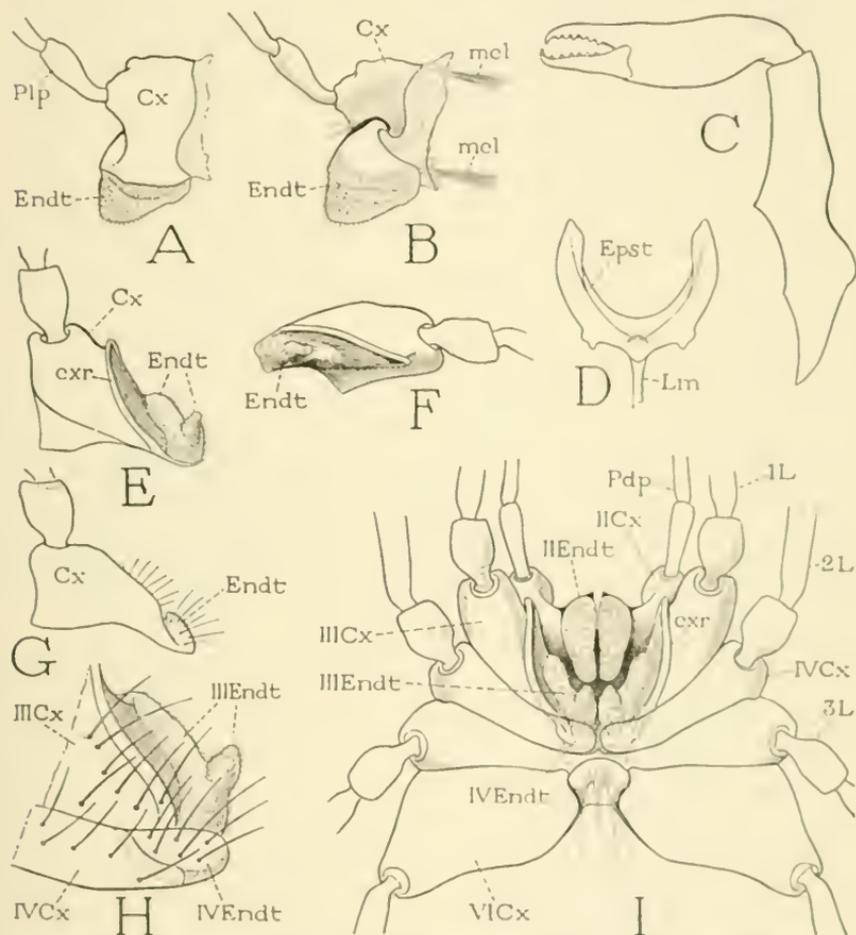


FIG. 15.—Phalangida-Cyphophthalmi, *Holoosiro acaroides* Ewing.

A, base of left pedipalp, lateral. B, base of right pedipalp, mesal. C, left chelicera, lateral. D, epistome and part of labrum, dorsal. E, base of right first leg, ventral. F, same, mesal. G, base of right second leg, posterior. H, details of mesal ends of coxae of right first and second legs more enlarged, ventral. I, bases of prosomatic appendages, except chelicerae, showing mouth parts, ventral. (All figures except H same enlargement.)

nature (*IVEndt*) that somewhat overlap the inner ends of the first-leg coxae. When the coxae of the second legs are detached and viewed from behind (G) the endites are seen to be distinct lobes, though their surfaces are hard and not membranous.

Since there are no sternal plates on the prosoma of the Cyphophthalmi, there is no under-lip structure closing the stomotheca below, such as the sternum of the first-leg segment in Phalangiidae. When the chelicerae are deflexed, however, their chelae are turned posteriorly, upside down, close against the endites of the pedipalps and the first legs; in this position the pincers fit neatly between the ridges of the first-leg coxae, and completely cover the stomotheca from below. During feeding, therefore, prey held in the chelicerae could thus be applied directly to the cleft between the pedipalp endites, through which the exuding juices might be drawn up to the mouth.

The suborder Palpatores, or Plagiostethi, includes the familiar long-legged phalangiids of the family Phalangiidae. The first full description of one of these arachnids goes back to Tulk (1843), who gives a detailed account of the external and internal structure of *Phalangium opilio* L. Tulk cites earlier writers but says their work is either superficial or lacking in detail. Among more recent papers those by Police (1927), and by Kästner (1933a) on the feeding organs of *Opilio* and *Phalangium* are the most important. Since Police critically reviews the work of others before his time, and gives numerous quotations from their descriptions, the student historically interested is referred to his paper. The following account of the phalangiid mouth parts as developed in the family Phalangiidae is based on a species of *Leiobunum*.

A front view of the body of a phalangiid (fig. 16 B) presents a most unusual appearance for an arachnid because of the number of structures that are associated with the mouth, but which entirely conceal it. Uppermost is the slender, tapering labrum (*Lm*) projecting as a free lobe from an epistomal plate (*Epst*) between the pedipalp coxae (*IICx*). Immediately below the labrum and converging beneath it are the large, soft, endites of the pedipalp coxae (*IIEndt*), each with a pair of accessory lobules on its base; and beneath these endites are the thick, padlike endites of the first pair of legs (*IIIEndt*). Below all these structures, projecting like a broad under lip, is the sternal plate of the first leg segment (*IIIS*), which forms the floor of the preoral cavity. Finally, projecting beneath the sternum are seen the small, hairy endites of the second-leg coxae (*IVEndt*).

The chelicerae of *Leiobunum*, as in all the Phalanga, are three-segmented (fig. 16 A, *Chl*). The basal segments extend forward from the anterior body wall above the epistome, the distal segments with the relatively small pincers hang downward at the sides of the labrum. The base of each chelicera is produced into the body as a large apodemal extension from the lateral and ventral walls of the proximal

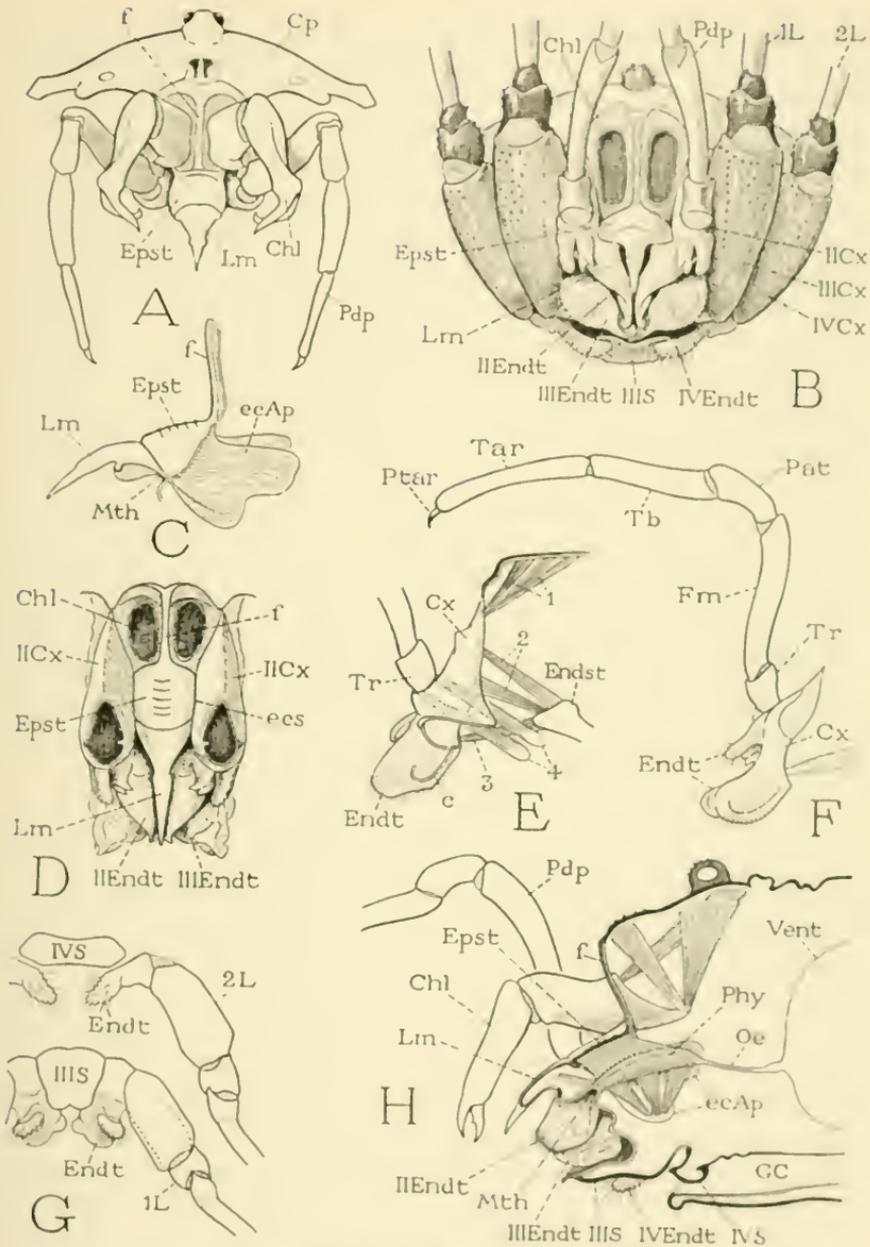


FIG. 16.—Phalangida-Palpatores, *Leobunum* sp.

A, anterior end of body with chelicerae and pedipalps. B, anterior end of body, chelicerae removed, turned dorsally to show mouth parts. C, labrum and epistome, with epistomocoxal apodemes, left side. D, mouth parts, anterodorsal view, chelicerae and telopodites of pedipalps removed. E, base of right pedipalp, with coxal endite and muscles, mesal view; c, "pseudotracheal" canal. F, left pedipalp, lateral. G, bases of first and second legs, with coxal endites and corresponding sterna. H, longitudinal section of anterior end of body, showing mouth parts of right side, mouth, and pharynx with its muscles.

segment, on which are inserted levator and depressor muscles arising on the carapace laterad of the eyes (H). Between the cheliceral bases a strong sclerotic bar (A, *f*) in the anterior body wall connects the epistome with the anterior edge of the carapace.

The pedipalp coxae are elongate dorsoventrally (fig. 16 D, *IICx*), as are the coxae of the legs (B). They are implanted in the membranous anterior wall of the body laterad of the chelicerae, and their upper ends, which reach almost to the level of the dorsal edges of the cheliceral bases (B, *Chl*), are weakly articulated on the anterior margin of the carapace. Mesally the dorsal walls of the pedipalp coxae are united with the lateral margins of the epistome (*Epst*), and along the line of union on each side (*ecs*) is inflected a broad, platelike epistomo-coxal apodeme (figs. 16 C, 17 C, *ecAp*). There is no median epistomal apodeme in *Leiobunum*. The musculature of the pedipalp coxa is the same as that of a leg in that it comprises dorsal muscles arising on the carapace (fig. 16 E, *1*), and ventral muscles (*2*, *3*) arising on the corresponding anterior arm of the endosternum (*Endst*). Each group of muscles includes mesal and lateral fibers representing the promotors and remotors of a leg. One of the ventral muscles of the pedipalp (*3*), being inserted on the base of the coxal endite, gives this flexible lobe an independent movement. The long muscles of the pedipalp trochanter (*4*) take their origins on the coxal lamella of the epistomo-coxal apodeme.

The endites of the pedipalps are broad, soft lobes, each with a pair of small lobules projecting anteriorly from its base (fig. 16 B, F). The flat mesal surfaces of these endites (E) are in apposition before the mouth (B, *IIEndt*). Each contains in its posterior part a slender, curved, deeply sunken groove (E, *c*) that runs up into the mouth. The groove is known as a "pseudotrachea" because of its finely ribbed walls, which give it the appearance of a trachea open along the outer side. The endites of the first legs (G, *1L*) are thick, soft, padlike lobes (B, H, *IIIEndt*) lying below the level of the mouth (H, *Mth*). Ventrally they come together under the pedipalp lobes where their extended margins overlap to form a gutterlike channel leading back toward the pharyngeal entrance (B). The small endites of the second legs (G, *2L*) project beneath the pedipalp sternum (B, H, *IVEndt*), and are too far removed from the mouth to have any direct relation to feeding, but they probably have a sensory function. According to Police (1927) each of the four endites associated with the mouth contains a pyriform, sacklike gland, the glands of the pedipalps opening on the dorsal margins of the mesal surfaces of the endites,

those of the first legs opening centrally on the inner surfaces. The nature of the secretion of these glands is not determined.

The mouth entrance of *Phalangium opilio* L. is described by Kästner (1933a, 1935) as a short funnel with its walls thrown outward in six radiating folds. The same region is termed the "buccal atrium" by Police (1927), who shows its structure in two cross sections (fig. 17 A, B). Both writers find that this region is provided with dorsal (anterior) muscles (A, *dld*) arising within the labrum, and ventral (posterior) muscles (*dlv*) arising on the epistomo-coxal apodemes. Police notes that the mouth atrium, therefore, can be dilated only in a vertical plane. Kästner says the mouth can be closed by the first circular muscles of the pharynx immediately behind it, and he regards the strong transverse muscle in the base of the labrum

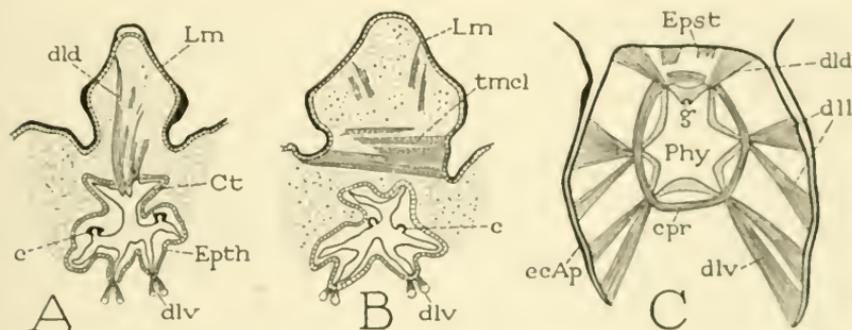


FIG. 17.—Phalangida-Phalangiidae, *Phalangium opilio* (Latr.).

A, cross section of labrum and mouth region, showing "pseudotracheal" canals (*c*) in walls of the latter (from Police, 1927). B, section through same parts farther back, showing transverse muscles of labrum (from Police, 1927). C, cross section through epistome, epistomocoxal apodemes (*ecAp*), and pharynx, showing groove (*g*) in dorsal wall of pharynx (from Kästner, 1933a).

(B, *tmcl*) as being also a closer of the mouth funnel, though, as Police points out, it would appear that this last muscle merely compresses the labrum. The six folds of the mouth, two dorsal, two lateral, and two ventral, are continued into similar folds of the walls of the pharynx (C, *Phy*). The pseudotracheal canals of the pedipalp endites (fig. 16 E, *c*) open into the lumina of the lateral mouth folds (fig. 17 A, B, *c*).

The pharynx of *Phalangium opilio* is said by Kästner to rise vertically from the mouth and then to turn abruptly backward in a narrowed horizontal part; in Police's figure of the same species the distinction between the two parts is much less accentuated. The pharynx of *Leiobunum* (fig. 16 H, *Phy*) is only slightly curved upward; it runs posteriorly between the large epistomo-coxal apodemes

(*ecAp*) parallel to the epistome (*Epst*), and is continued into the narrow oesophagus (*Oe*). On the crest of each of the six radial folds of the pharyngeal wall is inserted a row of dilator muscles (fig. 17 C). The dorsal muscles (*dld*) have their origins on the epistome (*Epst*); the lateral and ventral muscles (*dll*, *dlv*) arise on the epistomal lamellae of the epistomo-coxal apodemes (*ecAp*). Circular compressor fibers (*cpr*) alternating with the dilator muscles surround the entire length of the pharynx.

The dorsal wall of the pharynx of *Phalangium opilio* is shown by Kästner to be traversed by a narrow median groove with sclerotic walls (fig. 17 C, *g*). By contraction of the mouth region, Kästner says, the anterior end of the pharyngeal groove is brought into contact with the inner ends of the pseudotracheal canals of the pedipalp endites. The canal system, therefore, evidently has some unified function, though what this function may be is not known. It is of interest to note that a dorsal pharyngeal canal is present also in the Araneida (fig. 19 C, *dc*).

The oesophagus is a narrow tube (fig. 16 H, *Oe*) going direct from the end of the pharynx to the ventriculus (*Vent*). Just before joining the stomach the oesophagus is slightly enlarged, but apparently does not form here a sucking apparatus. According to Kästner the oesophagus lacks dilator muscles, and the circular muscles end where the tube enters the nerve mass.

In their feeding habits the phalangiids appear to be exceptional among the Arachnida in that they ingest fragments of their food as well as liquid. Hansen and Sørensen (1904) say that "the middle and anal divisions of the alimentary canal may be quite filled with more or less digested portions of food, fragments of animals which are easily recognized by the broken pieces of chitine which are contained in them; but such are never found in the diverticula." These writers did not mention any particular species. Police (1927) says that sections of *Phalangium opilio* show in the stomach only soft material, though this may contain fragments of viscera and tracheae. Tulk (1843) gives a rather fanciful description of the working of the mouth parts during feeding, in which the oral endites are conceived to be jaws for crushing the prey and extracting the juices, while a further crushing function is attributed to the pharynx. The pharynx, however, has no internal armature such as Tulk describes, and the oral endites, though independently movable on the supporting coxae, are too soft in texture to be masticatory organs. Though pieces of the internal organs of the prey may be taken into the stomach by the phalangiids, such fragments, according to Frank (1938), are dissolved

in the stomach, and the final digestive processes take place intracellularly within the stomach diverticula as with other arachnids.

Kästner (1925), in describing the observed manner of feeding by *Platybunus corniger* Herm. on a spider, says the captured prey is held in the chelicerae, and the abdomen first torn open. Then, while one of the pincers holds the cut edge, the other reaches into the opening and pulls out pieces of the entrails and brings them to the mouth parts. The fragments are seized by the coxal edites of the pedipalps and first legs, which open and close alternately and pass the food on to the mouth. After the meal, Kästner observes, both the chelicerae and the pedipalps, which latter have assisted in the act of feeding, are cleaned by drawing them through the oral lobes.

### IX. THE ARANEIDA

The spiders possess several features in the feeding apparatus by which they differ from the other arachnids. The two-segmented chelicerae have usually no process opposing the fanglike terminal segment, which closes against the basal segment. In all families except the Uloboridae the chelicerae contain poison glands. The pedipalp coxae, except in Liphistiidae and most of the Mygalomorphae, have large distal processes usually forming strong but immovable jawlike lobes. The lower lip, or floor of the preoral food cavity, is formed by the sternum of the pedipalp segment, which may be either free between the pedipalp coxae, or united with the sternal plate of the legs. The dorsal and ventral walls of the pharynx are more or less sclerotized, forming a strong dorsal plate and a more weakly developed ventral plate, the two connected laterally by membranes. The dorsal plate is traversed by a median channel running forward from the orifice of the oesophagus. The proventriculus is a strongly developed pumping organ, the so-called "stomach pump," and may be of more importance in the sucking function than the pharynx itself.

The cheliceral poison gland is a sacklike organ (figs. 19 A, 20 F) with a duct traversing the fang to open on the convex side of the latter near the point (fig. 19 A, *VPr*). In the Mygalomorphae the gland is contained entirely or mostly within the basal segment of the chelicera; in other groups it may project into the body cavity as far as the prosomatic nerve mass or beyond it. The gland is covered by a layer of muscle fibers; the fibers are said by Millot (1931) to be generally arranged spirally along the length of the sack, but to present variations and irregularities. In *Latrodectus mactans*, the highly venomous "black widow" spider, the muscles, as shown by Reese (1944), run longitudinally on the gland (fig. 20 F).

Glands contained in the pedipalp coxae and opening into the preoral food cavity are said to be present in all members of the Araneida; they are known as the *salivary glands*, or "maxillary" glands. According to Petrunkevitch (1933) these glands are unicellular in *Hypochilus*, but in all other genera they are multicellular sacklike organs, the number in each coxa varying with the species. In *Liphistius* and the Mygalomorphae the glands, as shown by Bertkau (1885) in *Atypus*, are distributed along the entire length of the coxa, and open irregularly on the upper surface near the inner edge. In other spiders the glands open on a small oval or circular area on the inner face of each coxa, known as the "sieve plate" because of its perforation by the duct orifices. A gland, or pair of glands, is present also in the labrum. The structure of the labral gland in *Atypus piceus* Sultzter is described in detail by Bertkau (1885), who says the gland opens on the outer surface of the labrum. According to Petrunkevitch (1933) there is apparently a pair of labral glands ("rostral glands") in all spiders, but in some they are so closely united as to appear to be a single organ. The two ducts discharge into a wide, slitlike atrium that opens to the exterior.

In the feeding of the spiders, extraoral digestion plays an important part. A powerful digestive fluid from the stomach is discharged on the prey and completely liquefies the soft tissues. So copious and effective is this exuded digestive fluid that some spiders are able to consume even small vertebrates, which they kill by the venomous bite of the chelicerae. In recording observations of the feeding of *Palystes natalius* (Karsch), a South African member of the Heteropodidae, on a small lizard, Warren (1923) says: "All the ordinary tissues, including tendons and cartilages, were rapidly softened, and the body became plastic, while the bones were completely disarticulated. The voluntary muscles and all the softer tissues dissolved with great rapidity when the out-flowing and in-flowing currents of digestive fluid gained access to them. After a period of about two and a half hours the body (about  $1\frac{3}{4}$  in. long) of the lizard had been reduced to a small, blackish, rounded and somewhat dry mass about  $\frac{1}{4}$  in. in diameter. This mass the spider allowed to drop to the ground." Abraham (1923) records the feeding of a species of *Thalassius*, family Pisauridae, on live fish, small frogs, and tadpoles. He describes the catching of fish in an aquarium by the spider, which holds to a rock by its long hind legs and plunges into the water to seize its victim. Baerg (1938) says of a large species of *Dugesia* (*Dugesia*) (*Aviculariidae*) that in captivity it will feed on recently killed animals, "accepting

besides various large insects, also crayfish, small lizards, small snakes, and even small fish."

A detailed account of observations on the feeding act of spiders is given by Kästner (see Gerhardt and Kästner, 1937, pp. 447-449). Some species, particularly those that feed on hard-shelled insects, such as beetles, merely suck out the dissolved tissues through a wound in the prey. Others, including most spiders, thrust the cheliceral claws into the body of the prey and tear the entrails to give the injected digestive fluid better access to the tissues; finally they crush and knead the prey in order to get the last juice from the mangled body. The digestive fluid is said by Kästner to be expelled repeatedly as a large drop of clear liquid that fills the preoral cavity of the spider and flows into the wound of the prey, and is then sucked back. The mechanical treatment of the prey, according to Kästner, is done entirely with the chelicerae, not with the jawlike lobes of the pedipalp coxae. The latter serve merely as the lateral walls of the space between the labrum above and the pedipalp sternum below, which is the food conduit from the prey to the mouth. During feeding, Kästner observes, a rapid extension and contraction of the labrum within the food conduit evidently exerts a preoral sucking action on the food liquid. The hard, insoluble parts of the prey, prevented from entering the mouth by the bristles of the coxae and sternum, accumulate in a mass on the lower lip and are finally dislodged by the pedipalps.

Earlier writers assumed the source of the exuded digestive liquid to be the glands of the pedipalp coxae, or so-called "maxillary" glands, but others have contended that the liquid is too copious to be produced in these relatively small glands, and must come from the stomach. Bertkau (1885) demonstrated experimentally that the secretion of the pedipalp glands does have a solvent effect on the muscles of a fly, but only after 24 hours was the muscle tissue reduced to a pulp, while a live spider dissolves the tissues of a fly often in a few hours. Kästner (see Gerhardt and Kästner, 1937, pp. 448-450) has shown from observation on a transparent *Theridium* species that during feeding there takes place a heaving and fluctuating movement of the alimentary mass in the abdomen, and that when a drop of fluid is discharged from the mouth the small end branches of the stomach diverticula contract and expand, suggesting that by this action the digestive juice is being expelled. From quantitative analyses of the digestive enzymes of *Arvicularia*, Schlottke (1936) demonstrated that no proteinase of sufficient strength to accomplish extraoral digestion is produced in any part of the spider anterior to the stomach. The stomach diverticula, according to Schlottke's results, secrete a strong

trypsinlike proteinase, an aminopolypeptidase, a carboxypolypeptidase, and a dipeptidase of varying strength. Lipase is strongly present, and amylase in some cases, but probably a part of the amylase comes from the prey. Since the several ferments are not found in the same amount in all individuals, it is evident that the diverticula do not secrete a uniform digestive liquid.

The Mygalomorphae (Orthognatha) differ from the other spiders, with respect to the feeding organs, in that the basal segments of the chelicerae are directed straight forward from the body, and that the pedipalp coxae, except in Atypidae, have only small, inconspicuous anterior processes instead of the large jawlike lobes present in most other spiders. As an example of the mouth-part structure in this group a species of *Eurypelma*, one of the "tarantulas" so called in America, is here described.

The pedipalps of *Eurypelma hentzi* Chamb. are smaller than the legs; in the female each appendage has six normal segments (fig. 18 C) and a small, clawlike pretarsus (D, *Ptar*). The single elongate tarsal segment is padded on the ventral surface with a thick, velvety coating of small soft hairs (G, *Tar*), which distally form two apical lobelike tufts. The pretarsal claw arises from a padlike surface on the end of the tarsus (D), but is ordinarily almost concealed by the overhanging hairs, only its tip being visible in the notch between the apical tufts (G, *Ptar*). The claw is provided with the usual two pretarsal muscles, a levator, arising in the tarsus, and a depressor, arising in the tibia and patella with its fibers inserted on a long ventral tendon of the claw. In the male, the pedipalp ends with a sperm-carrying organ (fig. 18 E, *Ptar*), which clearly is a modified and specialized pretarsal segment, since, as Barrows (1925) has shown, two muscles are attached on its base, a levator (*lvptar*) arising in the tarsus, and a depressor (*dpptar*) in the tibia. The legs differ from the pedipalps in having two subsegments in the tarsus, and a pair of pretarsal claws.

The pedipalp coxae lie horizontally in the plane of the leg coxae, but they diverge anteriorly from the suboral sternum between their bases. Their mesal faces adjoin the epistome, but are connected with the latter only by membranous conjunctivae. In *Eurypelma* and most of the other Mygalomorphae the pedipalp coxae have small anterior processes at the inner sides of the trochanteral bases (fig. 18 C, F, *cxp*), but in Atypidae (H) these coxal processes are large, thick lobes (*cxp*) projecting beneath the chelicerae.

The huge chelicerae of *Eurypelma* (fig. 18 A, *Chl*) project forward but sag somewhat downward from the receding anterior wall of the body, which seems scarce able to support them. The fangs turn back-

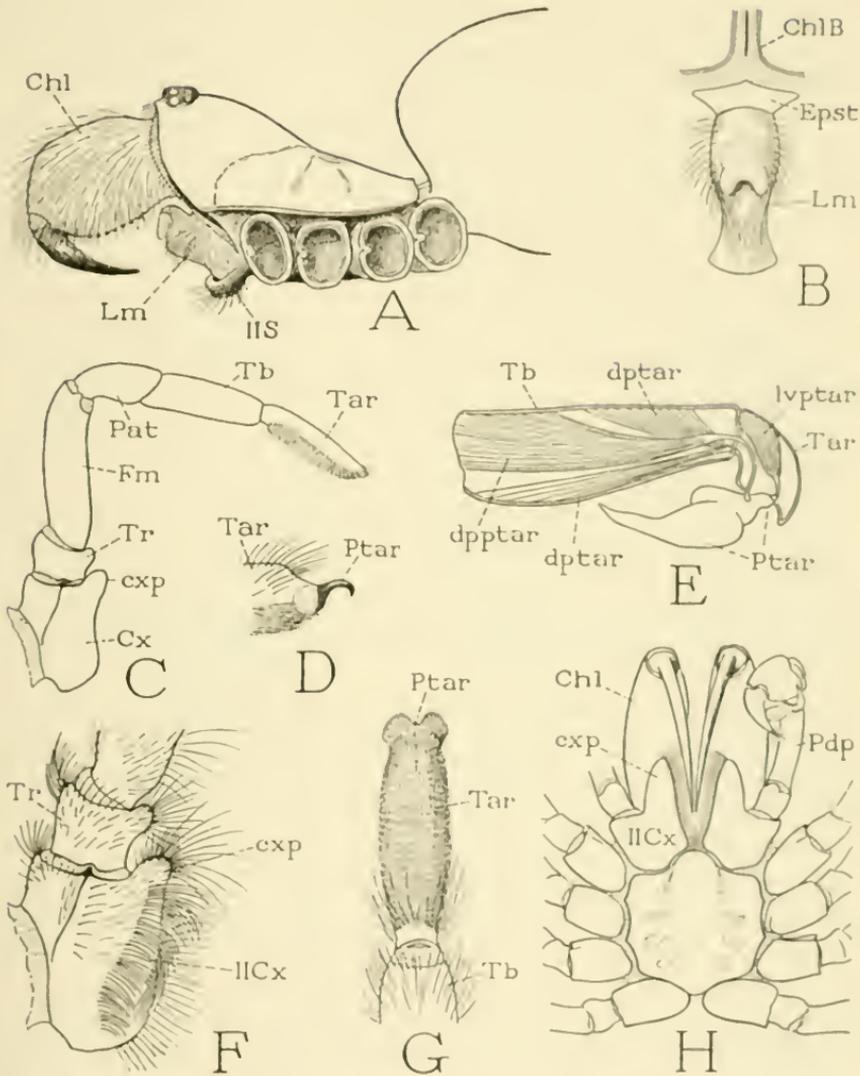


FIG. 18.—Araneida-Mygalomorphae.

A, *Eurypelma hentzi* Chamb., female, prosoma, with pedipalps and legs removed. B, same, epistome and labrum, anterior. C, same, left pedipalp, mesal. D, same, pretarsal claw of pedipalp exposed on end of partly denuded tarsus. E, *Eurypelma californica* Ausser, male, tarsus and pretarsus of pedipalp, with muscles (from Barrows, 1925). F, *Eurypelma hentzi* Chamb., female, basal part of left pedipalp. G, same, terminal segments of pedipalp, ventral. H, *Atypus bicolor* Lucas, prosoma and bases of appendages, ventral, showing large coxal processes of pedipalp coxae.

ward below the large basal segments. The venom gland of each appendage is an elongate, cylindrical sack (fig. 19 A) lying in the upper part of the basal segment. It is covered by a layer of flat, strongly striated muscle fibers, which go obliquely upward and posteriorly on each side, and their ends overlap along the midventral and middorsal lines. The duct traverses the fang to open by a pore (*VPr*) near the tip on the convex surface.

Beneath the chelicerae, the labrum (fig. 18 A, *Lm*) projects from the anterior wall of the prosoma in the form of a large, soft lobe with two small lobules on the angle between its short dorsal surface and the long, receding anterior surface. The sides are compressed (B) but expanded below to form before the mouth an upper lip fitting snugly into the concavity of the under-lip sternum (A, *IIS*). From the base of the dorsal surface of the labrum there is reflected upward in the body wall beneath the chelicerae a small, transverse epistomal plate (B, *Epst*) with prolonged lateral angles. The sternum of the pedipalp segment (A, *IIS*), which, as in all the Araneida, constitutes the under wall of the preoral cavity, is a small plate detached from the large sternal plate of the leg segments. As just noted, its concave upper surface receives the expanded lower end of the labrum.

Between the under surface of the labrum and the pedipalp sternum is the short preoral food cavity (fig. 19 B, *PrC*), which leads directly through the mouth (*Mth*) into the lumen of the pharynx (*Phy*). The pharynx slopes steeply upward behind the labrum and epistome, and the oesophagus (*Oe*) dips downward from its inner end. The walls of the pharynx are formed of an inwardly convex dorsal plate (*dpl*) and a concave ventral plate (*vpl*) united along their edges by membranous conjunctivae. The strongly sclerotic dorsal plate (C) is continued from the under surface of the labrum (*Lm*), the larger but weaker ventral plate (E) from the upper surface of the deutosternum (*IIS*). The dorsal plate (C) presents a high, rounded median lobe, flanked by two narrow lateral lobes. The middle lobe is deeply incised at its inner end, but a median arm is continued through the emargination. Traversing the middle lobe from the end of the arm almost to the labrum is a median channel (C, D, *dc*) with strongly sclerotic walls. At its upper (posterior) end the channel is widely open before the mouth of the oesophagus, but along the arm of the plate it is nearly closed by lateral folds of membrane, and then becomes again an open groove that tapers to a narrow slit ending shortly behind the labrum. On the dorsal plate of the pharynx is

attached a large dilator muscle (B), the fibers of which spread from their origins on the epistome (*Epst*).

The relatively weak, concave ventral plate of the pharynx (fig. 19 E) is longer than the dorsal plate because the edge of the pedipalp sternum (*IIS*) extends beyond the labrum. The median part of this plate, or ventral wall of the pharynx, is but weakly sclerotized except for a strong bar, deeply forked at the upper end, that traverses its middle. On the inner end of the ventral plate is inserted a pair of large muscles from the prosomatic carapace (B).

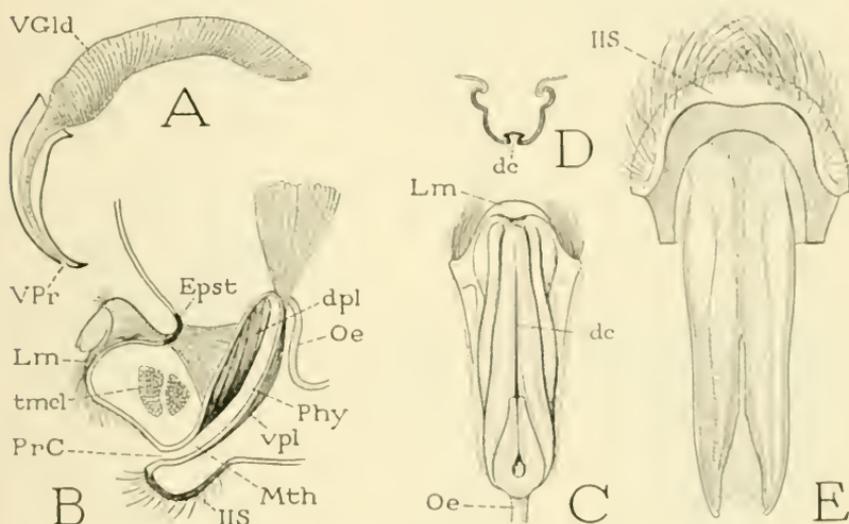


FIG. 19.—Aracnida-Mygalomorphae, *Eurypelma hentzi* Chamb.

A, cheliceral fang and venom gland. B, longitudinal section through mouth region and pharynx. C, dorsal plate of pharynx and lower end of labrum, ventral. D, cross section of dorsal plate of pharynx. E, ventral plate of pharynx and distal end of pedipalp sternum, dorsal.

The mouth parts of the Dipneumonomorphae (Labidognatha), or ordinary spiders, differ from those of the Mygalomorphae principally in that the chelicerae hang downward from the anterior edge of the prosoma (fig. 20 B), and that the pedipalp coxae have large lobes at the sides of the mouth which give the appearance of a pair of strong jaws (C, D, *cxp*). These coxal lobes of the spiders have no independent movement, since they are solidly affixed to the coxae. In appearance they suggest the coxal endites of the Phalangida, but inasmuch as they arise from the distal ends of the coxae, and in some forms, as in *Dysdera crocata* C. Koch (G), they are no different from the large coxal processes of the mygalomorph *Atypus* (fig. 18 H), it is clear that they are merely special developments of the

usual anterior coxal processes, such as those typical of the Mygalomorphae (fig. 18 C, F, *cxp*).

The labrum of the dipneumone spiders is a supraoral lobe of

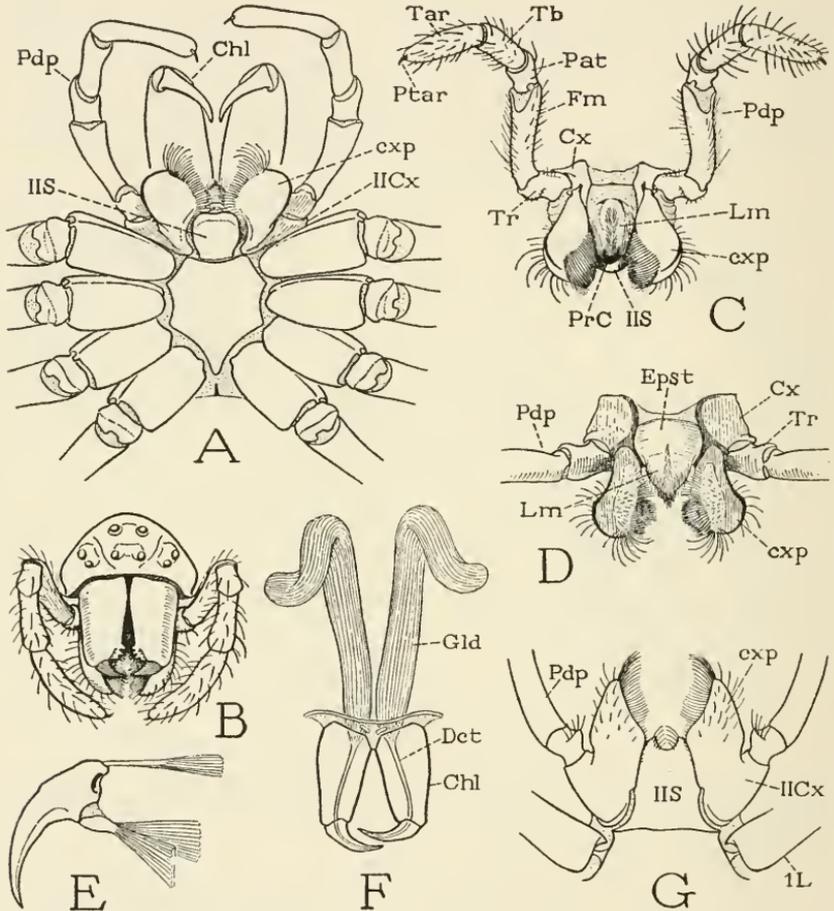


FIG. 20.—Araneida-Dipneumonormorphae.

A, *Heteropoda venatoria* L., Sparassidae, prosoma, with chelicerae, pedipalps, and bases of legs, ventral. B, *Metargiope trifasciata* (Forsk.), Argiopidae, female, anterior end of body. C, same, mouth region and pedipalps, anterior, showing preoral cavity (*PrC*) enclosed by labrum, coxal processes of pedipalps, and pedipalp sternum. D, *Heteropoda venatoria* L., epistome, labrum, and bases of pedipalps, anterior. E, *Metargiope trifasciata* (Forsk.), cheliceral fang and muscles. F, *Latrodectus mactans* Fab., Theridiidae, female, chelicerae with poison glands and ducts. G, *Dysdera crocata* C. Koch, female, Dysderidae, anterior part of ventral surface of body, with bases of pedipalps and first legs, showing large coxal processes embracing the suboral pedipalp sternum.

variable form and size (fig. 20 C, D; fig. 21 B, *Lm*) suspended from the epistome (fig. 20 D, *Epst*), which is united laterally with the pedipalp coxae (*Cx*). Between the labrum and the under lip formed

of the pedipalp sternum is a short preoral cavity (fig. 20 C; fig. 21 B, *PrC*) closed laterally by the lobes of the pedipalp coxae. The mouth at the inner end of the preoral cavity opens directly into the pharynx.

The pharynx rises steeply from the mouth behind the labrum and epistome (fig. 21 A, *Phy*). In a cross section of the pharynx of

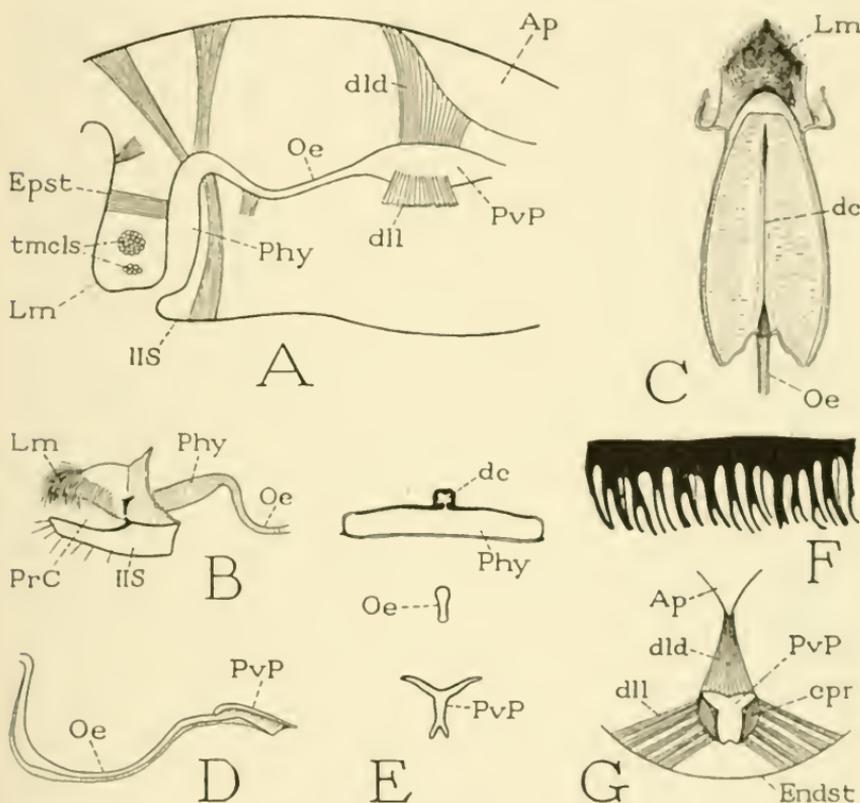


FIG. 21.—Aracnida-Dipneumonomorphae.

A, *Agelena naevia* Walck., diagrammatic longitudinal section of the prosoma, showing muscles of the stomodaeum (from Brown, 1939). B, *Dysdera crocata* C. Koch, labrum, pedipalp sternum, and pharynx, left side. C, *Heteropoda venatoria* L., labrum and dorsal plate of pharynx, ventral. D, same, oesophagus and proventricular pump, muscles removed. E, same, cross sections of pharynx, oesophagus, and proventricular pump. F, *Tegenaria domestica* (Cl.), longitudinal section of piece of dorsal plate of pharynx, showing transverse ridges, greatly magnified (from Bartels, 1930). G, *Agelena naevia* Walck., cross section of proventricular pump, with muscles (from Brown, 1939).

*Heteropoda venatoria* (E, *Phy*), the organ is seen to be much flattened dorsoventrally. In its dorsal (anterior) wall is a well-developed plate (C) traversed by a median channel (*dc*); the opposite wall is weak except for a sclerotized band along each lateral margin, which is connected by membrane with the dorsal plate. The channel of the

dorsal plate is widely open at its inner end before the oesophageal aperture (C), but beyond this point the lips are in such close apposition that the channel becomes practically a closed tube (E, *dc*), except that it opens again where it approaches the mouth (C). On each side of the median channel the surface of the plate is crossed by numerous fine ridges.

A longitudinal section of the dorsal pharyngeal plate of *Tegenaria domestica* (Cl.) (fig. 21 F), as given by Bartels (1930), shows that the surface ridges are high, thin folds of the cuticle, most of them forked along their free edges, between which are deep grooves. The grooves, Bartels believed, open mesally into the dorsal channel, though he was not able to demonstrate the apertures. In experiments on spiders allowed to drink water containing a suspension of India ink or carmine particles, he found the granules massed in the grooves and along the edges of the median channel, but very few in the channel itself, while only some of the smallest particles had gone into the stomach with the water. From these experiments Bartels concluded that the ridges of the pharyngeal plate constitute a filtering apparatus for the retention of undissolved material in the predigested food, while the liquid part enters the oesophagus by way of the grooves and the dorsal channel of the pharynx. The main lumen of the pharynx, according to Bartels, serves for the discharge of the digestive juices that first liquefy the soft tissues of the prey. However, inasmuch as with other arachnids the food is ingested through the pharynx lumen, it might be supposed that the dorsal channel of the Araneida serves as the conduit for the exuded digestive liquid; the very fact that the grooves of the dorsal plate become so readily clogged would seem to disqualify them as food conduits. A dorsal channel of the pharynx is present, however, also in the Phalangiidae, which are not known to practice extraoral digestion.

The musculature of the araneid pharynx includes the usual dilators arising on the epistome (fig. 21 A), and muscles attached on its upper end. It is shown by Brown (1939) that in *Agelena naevia* (A) there are two pairs of long dorsal muscles from the carapace, and a pair of ventral muscles from the pedipalp sternum, all attached on the upper end of the pharynx. The first dorsal muscle Brown calls a dilator of the pharynx, the second a retractor; the ventral muscle he terms a retractor of the "labium." Within the labrum are two transverse muscles (*tmcls*) as in most other arachnids.

The oesophagus curves downward and again upward from the pharynx (fig. 21 A, B, D), and expands to form a proventricular pump (A, D, *PvP*) before reaching the stomach. The oesophagus

of *Heteropoda venatoria* is laterally compressed (fig. 21 E, *Oe*); its dorsal wall is sclerotized and its ventral wall membranous (D). The proventriculus is Y-shaped in section (E, *PvP*), with the membranous lower wall of the stem inflected. A section of the proventricular pump of *Agelena naevia* (G), as figured by Brown (1939), shows strong sets of dilator muscles arising dorsally (*dld*) on an apodeme (*Ap*) of the carapace, and lateroventrally (*dll*) on the endosternum (*Endst*); compressor muscles (*cpr*) unite the dorsal and ventral folds of the proventricular wall.

#### X. THE ACARINA

The distinctive feature relating to the feeding apparatus of the Acarina is the presence of a discrete head structure carrying the mouth parts, known as the *capitulum*, *capitellum*, or *gnathosoma*. The first term is adopted here as being more generally used than the others. The capitulum projects in front of the part of the animal that bears the eyes, when eyes are present, and hence does not include the entire head region derived from the cephalic lobe of the embryo (fig. 1 E, *HL*). The acarine capitulum is simply a special development of the part of the cephalon that lies before the carapace in other arachnids, together with the chelicerae and the pedipalp coxae. The capitulum is more or less retracted into a recession of the body behind it, within which it is attached by a flexible conjunctiva that allows of retraction and protraction. The socketlike cavity that receives the base of the capitulum is commonly called the "camerostome," but the etymological significance of the term in this connection is not clear.

The essential thing that differentiates the capitulum of the Acarina (fig. 22 A) from the head of a spider or other arachnid (fig. 2 A) is the sclerotization of the cephalic wall above the bases of the chelicerae to form a dorsal fold or plate (fig. 22 A, *Tect*) projecting from beneath the anterior edge of the dorsum of the body (D). This plate, termed "rostrum" and "epistome," may more appropriately be named the *tectum* (*tectum capituli*), since it forms the dorsal wall, or "roof," of the capitulum. Laterally the tectum is fused with the dorsally extended basal angles of the pedipalp coxae (*IICx*), which are united with each other ventrally, so that there is thus formed a continuously sclerotized ring, the *basis capituli*. The coxae bear the palps (*Plp*), and their dorsal surfaces, as in other arachnids, are united mesally with a subcheliceral epistomal plate (*Epst*), which bears the labrum (*Lm*) overhanging the mouth. The ventral wall of the capitulum is produced beneath the mouth and the labrum as a

median lobe (*Hst*) known as the *hypostome*. The hypostome appears to be formed by the union of anterior coxal processes, and is thus quite comparable to the similarly formed under lip of the Ricinulei (fig. 10 C). The hypostome is the floor of the preoral cavity, and

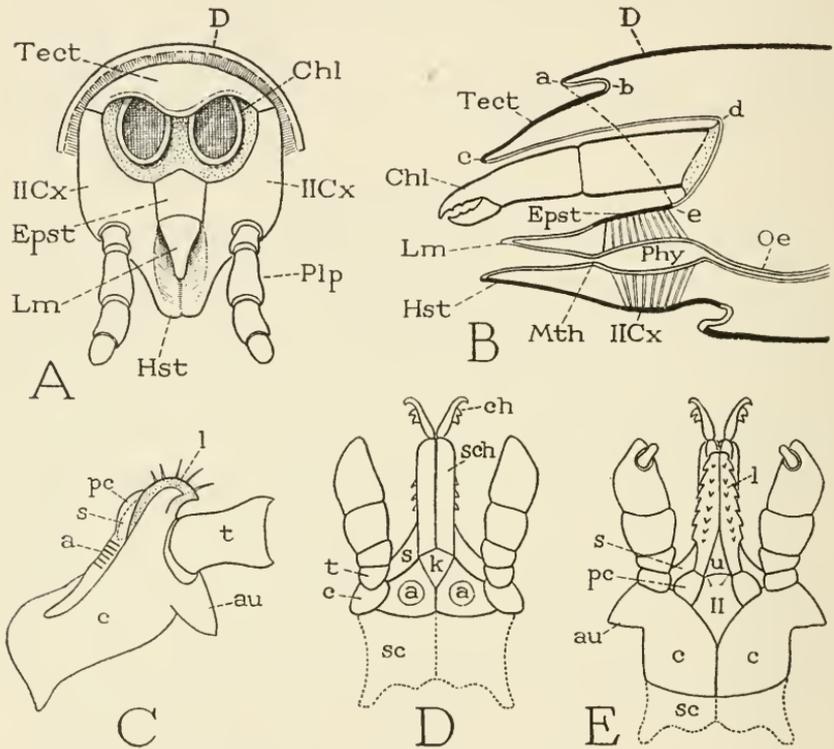


FIG. 22.—Acarina, structure of the capitulum.

A, diagrammatic anterior view of the capitulum, with chelicerae cut off at bases, showing lower lip, or hypostome (*Hst*), formed of united coxal processes (compare with A of figure 2). B, diagrammatic longitudinal section of anterior end of body (compare with D of figure 2). C, diagram of a primitive ixodid coxa according to Schulze (1935), showing parts that may enter into the formation of the capitulum: *a*, area porosa; *au*, auricle; *c*, coxa; *l*, coxal process; *pc*, processus cymatii; *s*, sella; *t*, trochanter. D, E, composition of the capitulum, dorsal and ventral, according to Schulze (1935): *ch*, chelicera; *II*, sternum; *k*, part of primary cephalic lobe; *sc*, subcoxa; *sch*, cheliceral sheath; *u*, hypopharynx; other lettering as on C.

its concave or grooved upper surface, more or less covered by the labrum, is the preoral food canal of the Acarina.

A lengthwise sectional view of the acarine capitulum (fig. 22 B) shows the tectum (*Tect*) as the outer wall of a fold (*b-c-d*) extended over the chelicerae, which latter thus appear to be sunken into a pouch of the head wall above the epistome. By comparison with a corre-

sponding section of any other arachnid it will be seen that the anterior cephalic wall in the Acarina, instead of going direct from the edge of the carapace to the base of the epistome, as in the spider (fig. 2 D, *a-e*), makes a complex folding (fig. 22 B, *a-b-c-d-e*) between the same two points. The mouth (*Mth*) between the base of the labrum and the base of the hypostome leads directly into the pharynx (*Phy*), which, as in other arachnids (fig. 2 D), has dorsal dilator muscles arising on the epistome (*Epst*).

To this simple basic structure of the capitulum there are added in the different groups of Acarina various secondary modifications, which may include the following: (1) a retraction of the capitulum into the anterior end of the body; (2) elongation, invagination, or other modifications of the chelicerae; (3) formation of membranous cheliceral sheaths; (4) invagination of the epistome; (5) reduction of the labrum; (6) elongation of the hypostome; (7) development of appendicular lobes on the pedipalp coxae associated with the hypostome; (8) reduction of the palps.

The exact composition of the acarine capitulum is perhaps more complex than that indicated above. However, Wagner (1894), in describing the embryonic development of *Ixodes calcaratus* Bir., ascribes the major part of the capitulum to the pedipalp coxae. The coxae, he says, are at first simple, but later a lobe grows out from each; then the coxae take a longitudinal position and their basal parts gradually grow upward around the bases of the chelicerae to form the capitular walls, while the lobes unite in an unpaired under-lip process (the hypostome). Reuter (1909) is more complete in his account of the development of the capitulum in *Pediculopsis graminum* (Reut.). The rudiments of the chelicerae and pedipalps, he says, undergo very great changes in the transformations by which these appendages, together with the cephalic lobe, are converted into the gnathosoma. The chelicerae undergo a considerable reduction and are transposed to a preoral position. The pedipalps are also reduced in their distal parts, but their basal parts embrace the chelicerae laterally, while ventrally they unite medially with each other, thus forming the lateral and ventral walls of the gnathosoma. The upper wall of this headlike structure, however, is derived from an unpaired projecting anterior part of the cephalic lobe, which unites laterally with the dorsal parts of the pedipalp coxae. The primary head lobe (Kopflappen), Reuter says, grows out between the proximal upper parts of the pedipalp coxae, and thus covers the cheliceral rudiments dorsally. "Dann verschmelzen die proximalen Teile der Pedipalpen unten median mit einander, oben mit den primären Kopflappen, wodurch ein vorn die

Mundöffnung enthaltendes, ringsum geschlossenes Gebilde entsteht." The simple structure of the capitulum in adult Notostigmata (fig. 23 A), as described by With (1904), is quite in accord with Reuter's account of the development in *Pediculopsis*.

Analyzing the capitular structure on a basis of comparative anatomy, Schulze (1932, 1935) contends that various elements besides the pedipalp coxae and the cephalic lobe enter into its composition. First, from a general study of the leg coxae of Ixodidae, Schulze deduces a concept of a primitive ixodid coxa (fig. 22 C) having an anterior process (*l*) projecting mesad of the trochanter (*t*), and an auricular lobe (*au*) on the outer angle. Along the anterior margin of the coxa a pleural fold, the "cymatium," is partly united with the coxa, but distally projects as a "processus cymatii" (*pc*) at the base of the anterior lobe. On the part of the cymatium adnate on the coxa is a porous area (*a*) of sense organs like those on the areae porosae of the capitulum. A small accessory fold (*s*) lies above the cymatial process.

The composition of the capitulum according to Schulze (fig. 22 D, E) is as follows: The pedipalp coxae ("Maxillae") form the major part of the basis capituli (Collare, or Kragen), but the trochanters must usually be included, since in certain ticks they appear as distinct basal segments of the palps (fig. 26 E, t). On the dorsal surface of the capitulum (fig. 22 D) the areae porosae (*a*) are derived from dorsomesal extensions of the porous areas of the coxal cymatia (C, *a*) united along the midline of the capitulum (D), while the small triangle (*k*) between their divergent anterior ends is formed from the primary cephalic lobe. On the ventral surface (E), the coxae (*c*, *c*) are united with each other proximally, but they embrace distally a plate (*II*) representing the deutosternum, which bears characteristically a pair of setae, and tapers distally in an "Unterlippe" (*u*) that forms the median basal part of the hypostome ("Clava"). The lateral toothed parts of the hypostome (*l*) are the anterior lobes of the primitive coxae (C, *l*) united with each other distally and with the sternal tongue between their bases. At the base of each coxal lobe of the hypostome appears the processes cymatii (E, *pc*), and laterad of this is a saddlelike piece, the "sella" (*s*), representing the small fold above the cymatium of the primitive coxa (C, *s*). Finally, a sub-coxal component is present as an invaginated extension from the base of the capitulum (D, E, *sc*). Schulze concludes with a tribute to the ingenuity of Nature, in that so many diverse parts can be brought together to form a unified structure for a specific purpose. We can

say only that it may be so, but that developmental evidence would be more convincing.

The mouth parts of the Acarina differ structurally from those of other Arachnida in no essential respect, as Börner (1902) has clearly shown. Recent writers, however, make no effort to correlate the acarine structure with that of arachnids in general, and their special terminologies become highly confusing: but, as Börner has said, since the mouth parts of the Acarina agree perfectly with those of other Arachnida, there is no need for the introduction of special terms for structures that already have generally applicable names. The review of the works of other writers that follows will show that the structural facts are fairly well known in several important acarine groups. The present writer has made no extensive study of the feeding organs of the Acarina, and, therefore, will attempt merely to bring the various published accounts together under a uniform terminology based on a concept of structural unity between the Acarina and other Arachnida. The terms used in the following descriptions may hence seem strange to acarologists, but few will deny the desirability of nomenclatural reform.

The only features of the acarine mouth parts that cannot be homologized with structures generally present in other Arachnida are the variously developed appendicular lobes or processes often associated with the distal part of the hypostome: lobes that are at least analogous with them, however, occur in the Chelonethida (fig. 12 A). These accessory hypostomal processes of the Acarina afford useful characters for specific descriptions, but each taxonomic writer usually has names of his own for them, or no names at all, and no attempt will be made here to invent a uniform terminology. The structures in question are evidently secondary lateral outgrowths of the coxal processes that are united in the hypostome; they are hence not "maxillary" processes, though in their various designations the maxillary idea seems to predominate. The structures might be called simply *hypostomal processes*. Usually, when present, there is a pair of them on each side, one member of which is lateral, the other mesal.

*Notostigmata*.—The capitulum and the mouth parts in this arachnid group, as described by With (1904), while in no sense primitive, show unquestionably an early stage in the evolution of the acarine capitulum. The tectum, termed "rostrum" by With, is a mere fold of the dorsal integument over the bases of the chelicerae (fig. 23 A, E, *Tect*), but it is united laterally with the high basal angles of the pedipalp coxae (A, *IIC.r*), and thus forms the dorsal wall of a primitive capitulum. From beneath the tectum project the large, fully exposed, three-

segmented chelicerae (*Chl*), which are but little invaginated at their bases. The chelicerae are typically arachnoid in form (D), and evidently are raptorial in function. Below the chelicerae is an elongate median plate (C, *Epst*) united laterally with the coxae and terminating in a free lobe that overhangs the mouth. With calls this entire plate "labrum," but he says it consists of a distal and a proximal part.

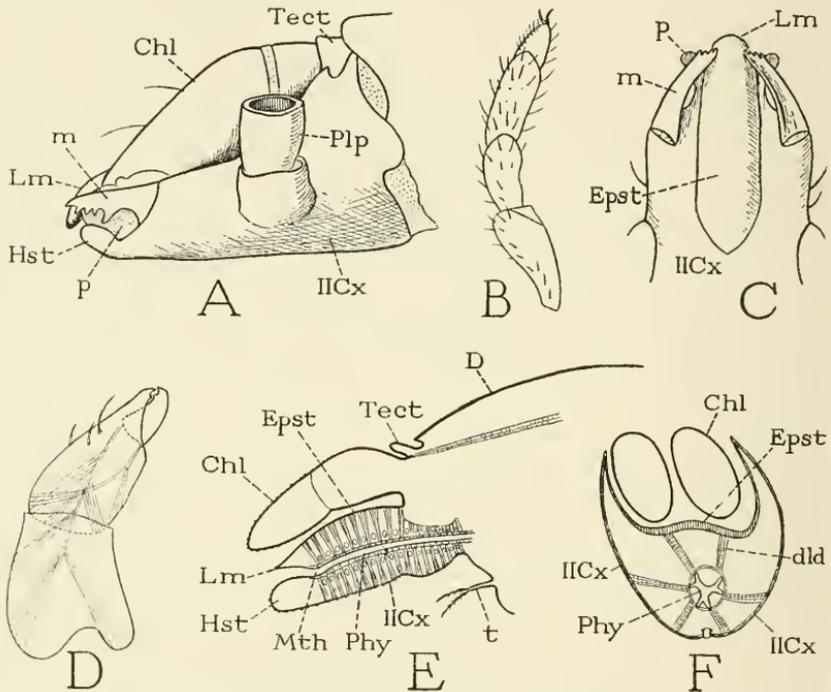


FIG. 23.—Acarina-Notostigmata, *Opiliacarus segmentatus* With (from With, 1904).

A, capitulum, left side: *m*, *p*, coxal lobes associated with the hypostome; *Tec*, tectum, or dorsal wall of capitulum. B, telopodite (palp) of pedipalp. C, dorsal surface of anterior part of capitulum below the chelicerae, showing apical lobes of coxae (*m*, *p*) and long epistomal plate (*Epst*) united laterally with the coxae. D, left chelicera, mesal. E, longitudinal section of capitulum and anterior end of body. F, transverse section of capitulum through pharynx, anterior to the tectum (E, *Tec*).

Since the proximal part is united with the pedipalp coxae and gives insertion to the dorsal muscles of the pharynx (E, F) it is clearly the epistome (C, E, F, *Epst*); the free apical lobe is the labrum (C, E, *Lm*).

The smooth, rounded under surface of the capitulum is extended forward beneath the labrum and ends in a pair of suboral lobes (A) that constitute the hypostome (A, E, *Hst*). At each side of the

hypostome is a pair of appendicular processes. In *Opiliacarus segmentatus*, as described by With, the outer process of each pair (*A, m*) is a toothed lobe articulated on the coxa, and is termed by With the "maxillary lobe"; the inner one (*f*) is a thin lamella distinguished as the "maxillary plate." The palps of the notostigmatid pedipalps are four-segmented beyond the coxa, and each bears a pair of pretarsal claws.

Proximal to the capitulum there projects from the ventral surface of the body a median bifid process (fig. 23 E, *t*), which is apparently a secondary development on the sternal region of the first-leg segment. Some writers term this structure the "labium," but the similar appendage in *Gamasides* was designated a "Bauchtaster" by Kramer (1876), who showed it has nothing to do with feeding, but probably has some function in connection with mating, since the genital orifice lies immediately behind it.

*Oribatoidea*.—In the scheme of acarine classification the sarcoptiform mites are not related to the Notostigmata, but the sectional figure by Berlese (1897) of the capitulum of a species described as *Oribates globulus*, probably *Euzetes seminulum* (O. F. Müller), given here at A of figure 24, shows a remarkably generalized condition of the mouth parts in combination with a well-developed capitulum. The tectum (*Tect*) is long and completely covers the retracted chelicerae (*Chl*). The short, two-segmented chelicerae, however, are typical chelate appendages, and, as shown in the figure, are merely invaginated beneath the tectum, so that each is contained in a pocket of the head wall inflected dorsally from the distal margin of the tectum, and ventrally from the base of the epistome (*Epst*). The epistome and the labrum (*Lm*) are together termed "labrum" by Berlese, but the epistomal region is clearly identified as such by the attachment on it of the dorsal pharyngeal muscles (*dld*), while the labrum is the free terminal lobe (*Lm*) projecting over the mouth. The ventral wall of the capitulum projects beyond the mouth (*Mth*), forming a short under-lip structure, or hypostome (*Hst*), with a median suboral lobe and a pair of lateral lobes. The pharynx (*Phy*) is of the usual structure. If this is a true picture of the oribatid structure, the latter is typically arachnoid except for the presence of the long dorsal wall of the capitulum, which covers the chelicerae, and this feature is merely an exaggeration of the structure in the Notostigmata.

*Holothyroida*.—In this group, as in the Parasitiformes, the chelicerae are elongate, deeply invaginated, and each is invested in a specific tubular sheath. The capitulum of *Holothyryus braueri* (fig. 24 B), as described and figured by Thon (1906), is covered dorsally

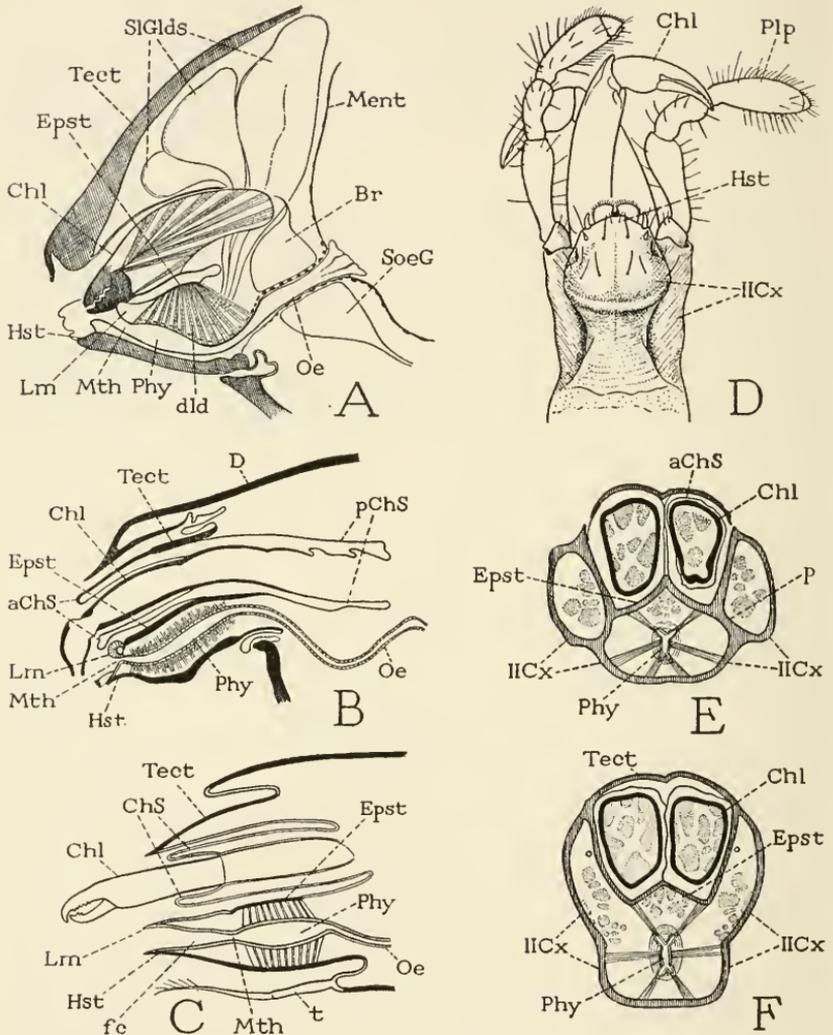


FIG. 24.—Acarina-Oribatoidea, Holothyroidea, Gamasides.

A, *Euzetes seminulum* (O. F. Müller), Oribatoidea, longitudinal section of capitulum (from Berlese, 1897). B, *Holothyrus braueri* Thon, Holothyroidea, longitudinal section of capitulum and anterior end of body (from Thon, 1906). C, *Poccilochirus carabi* Cn., Gamasides, diagrammatic representation from sagittal section of capitulum of male nymph by Winkler (1886). D, *Holothyrus braueri* Thon, Holothyroidea, capitulum, with palps and chelicerae (from Thon, 1906). E, same, cross section of anterior part of capitulum (from Thon, 1906). F, same, cross section of posterior part of capitulum (from Thon, 1906).

by a long duplicature of the prosomatic dorsum (D). The chelicerae (*Chl*), in the retracted state, are invaginated far into the body from between the tectum (*Tect*) above and the epistome (*Epst*) below. According to Thon the chelicerae are five-segmented, but since he says only two joints are articulations, it is evident that they are really three-segmented. The anterior parts of the cheliceral sheaths (*aChS*) are double tubular folds. The fold forming each outer sheath is extended dorsally from the tectum (*Tect*) and ventrally from the base of the epistome (*Epst*) to the end of the cheliceral shaft, where it is invaginated into itself to form the inner sheath more closely investing the chelicera and attached to the latter on the end of the basal segment. Thon describes also posterior cheliceral sheaths (B, *pChS*) reflected dorsally from the inner part of the tectum and ventrally from the epistome; but a posterior ensheathment of this kind is difficult to understand morphologically, and Thon, himself, says it probably results from some secondary modification.

The long epistomal plate of *Holothyryus* (fig. 24 B, *Epst*), called "labrum" by Thon, underlies the cheliceral sheaths and gives attachment to the dorsal muscles of the pharynx (E, F, *Phy*); laterally it is united with the mesal walls of the pedipalp coxae (E, *IICx*). Distally the epistome bears a small spiny lobe (B, *Lm*) overhanging the mouth (*Mth*). The interior of the lobe is filled with radiating columns of fibrous tissue, and the organ is provided with a pair of depressor muscles arising on the epistome. This movable, spine-covered lobe evidently has a rasping function, and for this reason Thon calls it the "Radularorgan"; there can be no question, however, that it is the labrum in an unusual form.

The lower wall of the capitulum of *Holothyryus* (fig. 24 D) has a three-lobed appearance owing to lengthwise indentations along the sides (E, F). Anteriorly the coxal cavity is divided into three compartments by partitions (E, *p*) inflected from the margins of the epistome to the coxal grooves, but posteriorly the partitions are absent (F). The distal end, or hypostomal region, of the ventral wall of the capitulum (D, *Hst*) bears a pair of broad median lobes and a pair of small lateral processes suggestive of the four apical appendages in the Notostigmata. The relatively long palps (D, *Plp*) are five-segmented but appear to lack pretarsal claws.

*Gamasides*.—The capitulum is said by Winkler (1886) to be well developed in all Parasitidae, but ventrally the segment of the first legs closely adjoins the capitulum (fig. 25 A, B) and projects with it from the anterior cavity of the body. A bifid ventral process (*t*) arises from the tritosternal region as in Notostigmata. The chelicerae are

long, three-segmented, and chelate (fig. 24 C, *Chl*). Each chelicera is invested in a membranous sheath (*ChS*) inflected from the distal end of the tectum and the inner end of the epistome, and then reflected forward in a fold that again turns back within itself to the distal end of the basal segment of the contained chelicera.

The diagram here given (fig. 24 C) is a free translation of the essential structure in Winkler's sectional figure of a male nymph of *Poecilochirus carabi* Cn. Below the chelicerae are the epistome (*Epst*), termed the "intermaxillary Chitingerüst" by Winkler, and the elongate labrum (*Lm*). The labrum ("Zunge"), Winkler says, is movable up and down, and also retractile by muscles inserted on its base, and is pressed like a wedge into a groove of the hypostome.

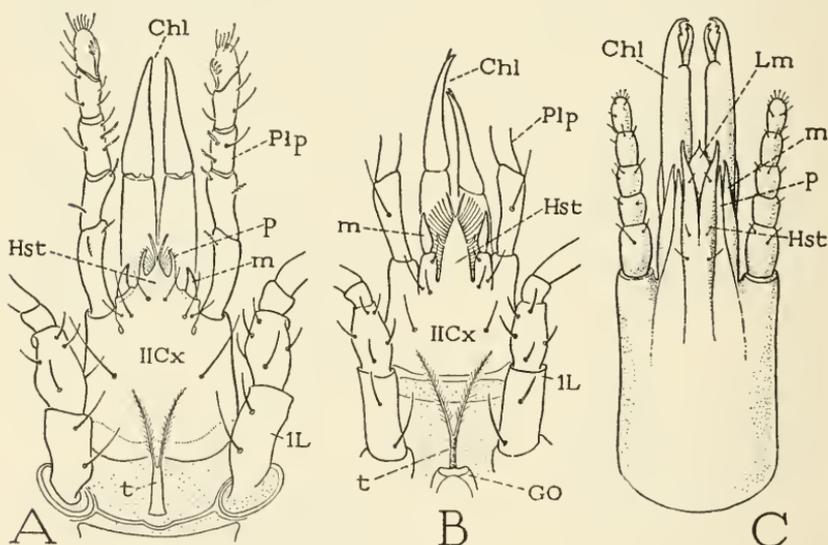


FIG. 25.—Acarina-Gamasides.

A, *Parasitus crassipes* (L.), female, capitulum and first body segment, ventral (from Winkler, 1886). B, same, male (from Winkler, 1886). C, *Laclaps echidninus* Berl., capitulum, ventral (from Stanley, 1931); *m*, *p*, coxal processes associated with the hypostome.

The under surface of the capitulum is prolonged beyond the mouth into a hypostomal under-lip structure (fig. 24 C, *Hst*). In *Parasitus crassipes* (L.) figured by Winkler (fig. 25 A, B) the hypostome presents a median lobe fringed with long hairs, which is much longer in the male (B) than in the female (A), and bears on each side a slender process (*p*) and a small lateral lobe supporting a knifelike or scalpel-shaped process (*m*). These hypostomal details, Winkler says, show much variation in different species.

The paper by Steding (1924) on *Halarachne otariae* Sted., a species found in the nasal cavity of the California otter, does not give much concise information on the mouth parts, and the figures are somewhat sketchy, but the structure evidently is not essentially different from that of other Gamasides. The chelicerae are said to be enclosed in sheaths, but the sheath connections are not shown in a sectional view of the head. A subchelicerai epistomal plate is clearly depicted in a cross section, giving attachment to the dorsal muscles of the pharynx. The term "Oberlippe" evidently refers to the tectum, since Steding says it is a prolongation of the dorsal edge of the body, but the true labrum is seen in a sectional figure as a lobe projecting over the mouth from the epistome.

The description of the mouth parts of *Laelaps echidninus* Berl. given by Stanley (1931) presents some details more clearly than the earlier papers on Gamasides, but in certain respects it is difficult to understand, and the terminology is confusing. The chelicerae are called "mandibles," the dorsal wall of the capitulum (tectum capituli) is said to be prolonged in a long, flaplike "epistome"; the large labrum, with its ventral surface continuous into the dorsal wall of the pharynx, is termed the "lingula," and a long dorsal lobe of the labrum is named the *vomer*. The under surface of the vomer is described as being grooved and fitting over a dorsal ridge of the "lingula." The vomer is a structure not described by other writers. The chelicerae are said to be enclosed in sheaths, but the connection of the sheaths with surrounding parts are not clearly shown. The long hypostome is split into two tapering lobes (fig. 28 I, *Hst*), and from the coxal area at each side of it arise two slender, sharp-pointed processes. The lateral process (*a*) Stanley calls the "stylus," the mesal process (*b*) the "maxilla"; the two processes on each side are loosely locked together by a ridge on the "stylus" received into a groove of the "maxilla."

*Ixodidae and Argasidae.*—The ticks have a well-developed capitulum with strongly sclerotic walls (fig. 26 A-D); a wide basal extension (lined in the figures) fits into the so-called "camerostome," and is mostly covered in the retracted position of the head (C). On the exposed dorsal surface proximal to the palps in the female are two *areae porosae* (A, *ap*), presumably sensory. Between the palps the capitular wall is prolonged into the dorsal walls of tubular sheaths (*Chs*) enclosing the chelicerae. The ventral wall of the capitulum (B, C) is extended between the palps to form the large hypostome (B, *Hst*), which may be parallel-sided or somewhat spoon-shaped, and is generally armed below with strong retrorse teeth. The cheliceral sheaths with the contained chelicerae, and the hypostome constitute

a veritable *rostrum*, from the end of which project the movable, laterally toothed digits of the chelicerae. The upper concave surface of the hypostome has a median gutterlike groove (fig. 28 J, K, *hg*) that leads back to the mouth and is the floor of the food conduit within the rostrum.

The palps are freely movable on the capitulum. Each consists typically of four segments (fig. 26 A, B), of which the first is a small basal ring, the second and third are long and broad, while the fourth is a small hairy pad or papilla set in a membranous area on the mesal side of the end of the third segment (B, C, G, H). In *Dermacentor*, however, the apparent basal segment of the palp (C) is immovably united with the second segment, and in *Boophilus* (G) a basal segment is not distinguishable from the second. In the females of certain species of *Endopalpiger* from New Guinea and Australia, Schulze (1935) has shown that the basal segments of the palps are produced into large lobes embracing the rostrum (E, *t, t*). These segments Schulze regards as the trochanters of the pedipalps, which in other species and in the males of these same species are supposed to be incorporated in the capitulum, the long third segment of each palp, being interpreted as the usual second and third segments united. A smaller lobe arising from the base of the palp in *Ixodes auritulus* Newm. (F, *l*), however, is regarded by Schulze as pertaining to a secondarily separated proximal ring of the first segment. Superficially, it is not clear that this lobe and the supposed trochanters of *Endopalpiger* are not equivalent structures, and it seems strange that free trochanters should be retained only in the females of a few species.

The chelicerae of the ticks are long shafts deeply buried in the capitulum, or even projecting beyond the capitulum into the body, and each is enclosed in a membranous sleeve-like sheath. Distally each chelicera bears a free, strongly toothed segment, or *digit*, movable by a pair of antagonistic muscles arising in the shaft, and therefore representing the movable finger of a typical chelicera. The digit consists of two principal parts (fig. 26 J, K); one is a rigid prolongation (*a*) from the base of the segment, with a pair of outwardly directed teeth at its apex; the other (*b*) is a broad lateral lobe with two large teeth, flexibly attached to the side of the fixed process. In *Ixodes* (I) there is a third, dorsal process, but in some other genera as in *Amblyomma* (J) and *Dermacentor* (K, L), a large, thin membranous fold (*c*) arises dorsally from the base of the digit and covers the toothed processes. Finally, the end of the cheliceral shaft is produced into a hoodlike protective lobe (*h*) on the mesal side of the digit. The digits move in a transverse plane on the ends of the shafts,

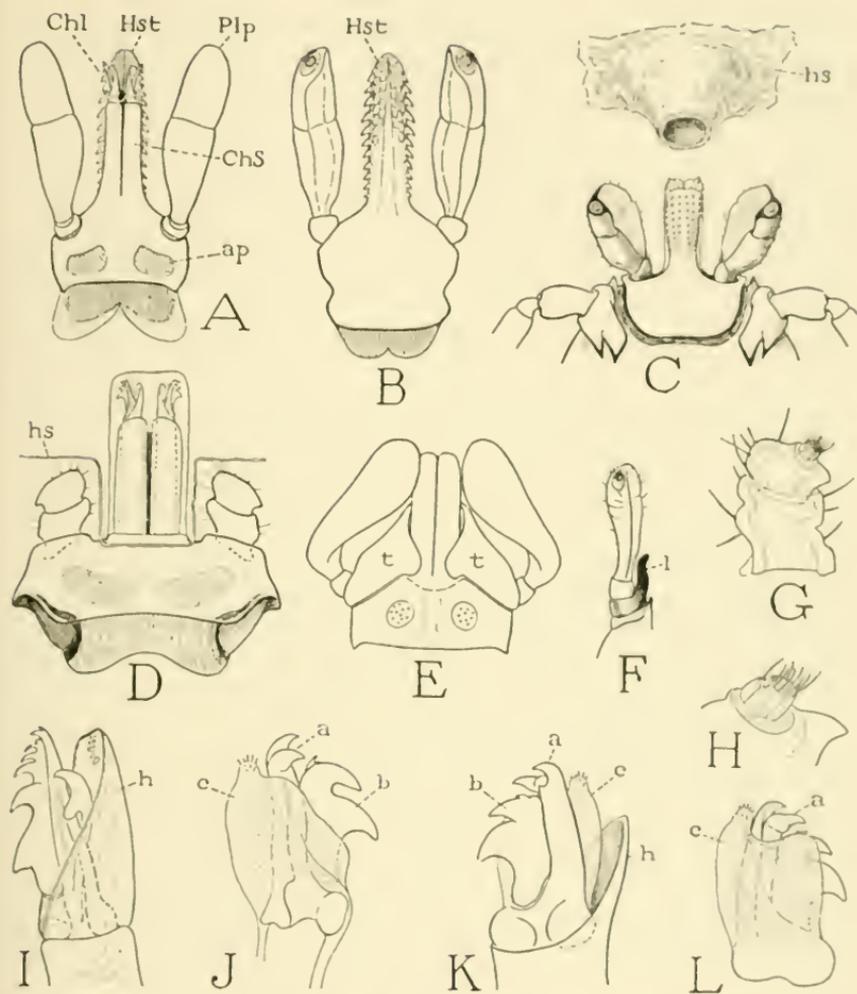


FIG. 20.—Acarina-Ixodidae.

A, *Ixodes ricinus scapularis* Say, capitulum, dorsal. B, same, capitulum, ventral. C, *Dermacentor variabilis* (Say), capitulum and first legs, ventral, and papilla of host's skin from which the rostrum of the tick was extracted. D, *Boophilus annulatus microplus* (Can.), capitulum, dorsal; *hs*, outline of skin of host ensheathing the rostrum. E, *Ixodes (Endopalpiger) tasmani victoriae* Schulze, female, capitulum, dorsal, showing large basal lobes (*t, t*) of palps (from Schulze, 1935). F, *Ixodes auritulus* Newm., female, palp with basal lobe (*l*) (from Schulze, 1935). G, *Boophilus annulatus microplus* (Can.), palp. H, same, apical segment of palp. I, *Ixodes ricinus scapularis* Say, end of left chelicera, dorsal. J, *Amblyomma maculatum* Koch, right cheliceral digit, dorsal. K, *Dermacentor variabilis* (Say), end of right chelicera, ventral. L, same, digit of right chelicera, dorsal.

*a*, main shaft of cheliceral digit; *b*, toothed lateral lobe of digit; *c*, membranous dorsal lobe of digit; *h*, protective extension (hood) from shaft of chelicera.

so that the cutting action of their teeth is in a lateral direction. The shafts are protractile and retractile within the sheaths. On their bases are inserted the usual cheliceral muscles, which here serve as retractors; protraction is said to be produced by a bulblike compression of the body effected by the dorsoventral somatic muscles.

The exact method by which a tick "bites" perhaps needs more study than has been given to it. Sharif (1928) observes that the palps of a feeding tick are pressed against the skin of the host, and that the initial incision must be the work of the chelicerae, which cut the skin to admit the blunt tip of the hypostome and enable the latter to be pushed into the wound. According to Cooley and Kohls (1944) the hypostome in the argasid genus *Antricola* has only very small teeth, while the chelicerae are large and effective cutting organs. The mouth parts of these ticks, therefore, are "adapted for quick feeding and not for clinging to the host." In preserved specimens of *Dermacentor*, *Amblyomma*, and *Boophilus* that have been detached with a piece of the host's skin, the rostrum of the tick is ensheathed to its base in a conical or sleeve-like papilla extended from the flat surface of the integument, and the sides of the papilla are clasped by the concave mesal surfaces of the palps. Figure 26 C shows a papilla from which the rostrum of the tick below has been removed, and at D the line *hs* indicates the position of the papilla ensheathing the rostrum. If the papilla results from the forcible detachment of the tick, the teeth of the hypostome should be holding at its distal end; on the contrary, the hypostome in all cases is completely enclosed with its toothed extremity at the bottom of the tube. In these specimens, therefore, it would appear that the skin of the host has grown out around the rostrum of the tick. Portman and Dalke (1945) report finding numerous larvae, nymphs, and adults of *Amblyomma americanum* buried in the skin of a fox, presumably as a result of local swellings of the host tissue that had engulfed the parasites.

The ticks are said to have a keen sense of odor perception. In the Ixodidae the organs of smell, known as Haller's organs, are groups of innervated hairs in cavities on the tarsi of the first pair of legs. When these legs are amputated, according to Totze (1933), the tick gives no reaction to odor, but will feed through a moist, warm, artificial membrane on blood or most any kind of liquid, such as chemical solutions, even strong-tasting substances, showing that it has no gustatory sense. Presumably, then, the ticks recognize an animal as its proper source of food by a sense of smell, and the combination of warmth and moisture from the skin gives the stimulus for feeding.

The cheliceral sheaths are double-walled tubular folds of the capitular integument extended individually around the shafts of the chelicerae. In figure 27 the sheaths are represented diagrammatically as they are shown by Douglas (1943) in *Dermacentor andersoni*. The outer wall of each fold, or *outer sheath (oChS)*, is produced forward from the dorsal wall of the capitulum above (*Tect*), and from the base of the labrum (*Lm*) below to the end of the cheliceral shaft; it is then invaginated into itself to form an *inner sheath (iChS)* closely investing the chelicera. In *Dermacentor variabilis* the cheliceral sheaths appear to be the same as in *D. andersoni*, but in *Argas*

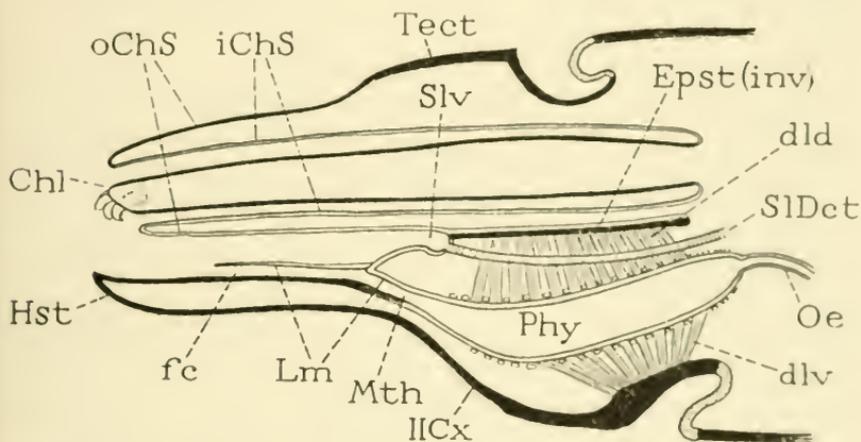


FIG. 27.—Acarina, diagram of the structure of the capitulum in longitudinal section.

*Chl*, chelicera; *dld*, dorsal dilator muscles of pharynx; *dlv*, ventral dilators of pharynx; *Epst*, epistome, invaginated; *fc*, food canal; *Hst*, hypostome; *IIcx*, pedipalp coxa; *iChS*, inner cheliceral sheath; *Lm*, labrum ("styletlike process"); *Mth*, mouth; *oChS*, outer cheliceral sheath; *Oe*, oesophagus; *Phy*, pharynx; *SIDct*, salivary duct; *Slv*, salivarium; *Tec*, tectum (dorsal wall of capitulum).

*persicus*, described by Robinson and Davidson (1913, '14), and in *Ornithodoros coriaccus*, described by True (1932), the lower wall of each inner sheath tube is said to be united for a part of its length with the upper surface of the subcheliceral plate (fig. 28 A, *Epst*).

The subcheliceral plate of the ticks is clearly the epistome (fig. 27, *Epst*), since it supports the labrum (*Lm*) at its distal end, and gives attachment on its ventral surface to the dorsal dilator muscles of the pharynx (*dld*). Inasmuch, however, as the ventral folds of the cheliceral sheaths arise at the base of the labrum in the Argasidae (fig. 28 A) it is evident that in these ticks the epistome is entirely invaginated. Christophers (1906), in fact, describes the epistome of *Ornithodoros* as an endoskeletal plate arising from a transverse bar

at the base of the labrum, composed of two strong lateral arms blended medially to form a long horizontal plate projecting freely into the body cavity. The subchelicerel plate of *Argas persicus* is said by Robinson and Davidson to be thin medially, but strengthened along the sides by marginal thickenings (fig. 28 L, *Epst*). The plate serves the dual purpose of furnishing a smooth surface on which the chelicerae slide, and of giving attachment ventrally to the dorsal dilator muscles of the pharynx (*dld*). The descriptions of *Ixodes ricinus* by Samson (1909), and of *Dermacentor andersoni* by Douglas (1943) are not specific concerning the nature of the epistome. Douglas makes the obscure statement that the buccal cavity "is formed in the subchelicerel plate," but in his figure A on plate 15 he shows dorsal muscles of the pharynx attached on subchelicerel sclerites, which must be the thickened lateral parts of an epistomal plate. True (1932) represents the subchelicerel plate of *Ornithodoros coriaceus* as given by Robinson and Davidson for *Argas persicus*.

From the end of the subchelicerel plate, or epistome, there projects over the mouth a small lobe (fig. 27, *Lm*), which is inserted into the widened proximal end of the gutter of the hypostome. Samson (1909) refers to this structure in *Ixodes ricinus* as a thin plate, shown in sectional view as a short flap extending over the mouth; Christophers (1906) observed it in *Ornithodoros savignyi*, but mentions it only as a small tongue protecting the pharyngeal orifice; Robinson and Davidson (1913, '14) describe the same thing in *Argas persicus* as a "tongue-like process," and show it in section as a tapering lobe (fig. 28 A, *Lm*) projecting over the mouth. Later writers have noted what appears to be a slender rod extending forward from the apex of the lobe, and have termed the whole structure the "styletlike process," or "tonguelike process" (fig. 28 E, *Lm*). Much has been written concerning the nature of this organ. Sen (1935) contended that the "stylet" is an open tube, the lumen of which is continuous into that of the pharynx, and that the mouth of the ticks is therefore a minute orifice at the apex of the stylet. Douglas (1943) accepts this interpretation, and represents the pharynx of *Dermacentor* as opening through the narrow tip of the stylet. Bertram (1939) and Arthur (1946), however, have shown that the stylet is an imperforate process projecting *above* the mouth, and normally lying over the gutter of the hypostome (fig. 28 J, *Lm*).

In *Ixodes*, *Dermacentor*, and *Amblyomma* the so-called "stylet" is long and slender; when pulled away from the hypostome there is usually to be seen attached to each side of it a narrow, very delicate membrane with an irregular and apparently broken margin (fig. 28 B,

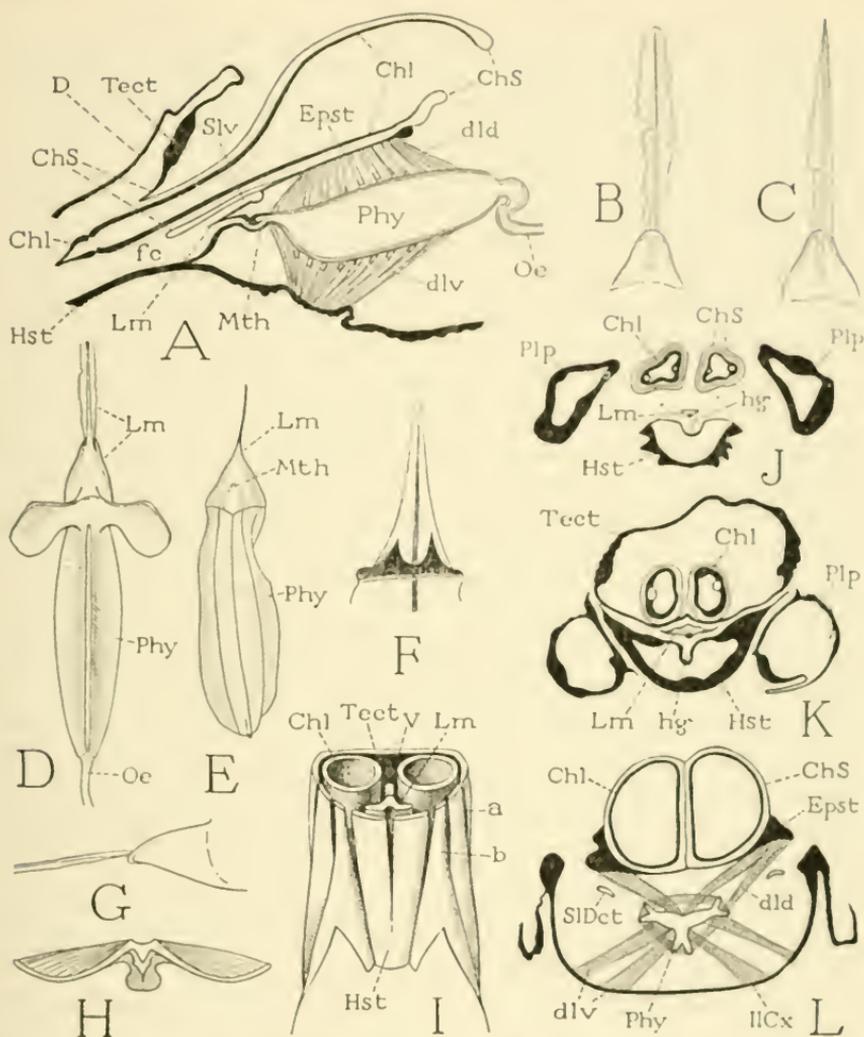


FIG. 28.—Acarina—Ixodidae, Argasidae, Laelaptidae.

A. *Argas persicus* (Oken), longitudinal section of capitulum (from Robinson and Davidson, 1913, '14). B, C, *Dermacentor variabilis* (Say), examples of the labrum as obtained by dissection (margins of apical blade broken). D, same, pharynx and labrum, dorsal. E, *Ixodes ricinus* L., pharynx and labrum, dorsal (from Arthur, 1946). F, *Ornithodoros tholozani* (L. and M.), labrum ("tongue-like process") (from Bertram, 1939). G, *Dermacentor variabilis* (Say), labrum, lateral. H, *Dermacentor andersoni* Stiles, anterior wing plates of pharynx with muscles, and section of oral aperture, posterior (from Douglas, 1943). I, *Laelaps echidninus* Berl., basal half of rostrum, ventral, showing arrangement of the mouth parts (from part of figure by Stanley, 1931); a, b, lateral processes of the rostrum. J, *Ixodes ricinus* L., transverse section of mouth parts and palps (from Arthur, 1946). K, *Argas persicus* (Oken), transverse section of capitulum at base of hypostome (from Robinson and Davidson, 1913, '14). L, same, transverse section of capitulum through pharynx (from Robinson and Davidson, 1913, '14).

C). The filamentous axial "stylet," in fact, is the midrib of a long, thin blade that covers at least the proximal two-thirds of the hypostomal gutter, the edges of which become torn by removal from the hypostome. Whether the marginal membranes are attached to the hypostome, or are merely closely adherent to it, the writer has not been able to determine by dissection; but Robinson and Davidson in their figure of a transverse section of the capitulum of *Argas persicus* (fig. 28 K) show the "stylet" (*Lm*) with wide lateral expansions lying free above the hypostomal gutter (*hg*), and the organ of *Ornithodoros* is very clearly depicted by Bertram as a flat tapering blade (*F*) lying over the proximal part of the gutter of the hypostome.

Considering the relations of the "styletlike process" of the ticks to the epistome behind it and to the mouth below it, there can be no question that the organ so called is the *labrum* (fig. 27, *Lm*); it corresponds exactly with the labrum of other arachnids, and in form is suggestive of the labrum of a phalangiid (fig. 16 D, H, *Lm*). Börner (1902) notes that the labrum of the Ixodidae is much reduced. The ixodid labrum, however, though small in size, is differentiated into a conical basal lobe, and a thin bladelike distal extension. The basal lobe overhangs the mouth; the apical blade, which varies in length in different species, lies over the gutter of the hypostome. The covered part of the hypostomal gutter is thus converted into a closed canal that leads back to the mouth, and this canal, as Bertram has shown, must be the food conduit (fig. 27, *fc*). Bertram (1939) gives a long discussion of the "tongue-like process" in *Ornithodoros*, in which he discards the impossible suggestion of Sen that the process corresponds with the hypopharynx of insects; it is difficult to see how he missed the obvious fact that the organ is the labrum.

A comparison of the mouth parts of the Ixodides with those of Gamasides in which the tapering labrum reaches to the end of the hypostome (fig. 24 C) will show the identity of structure in the two groups. The relation of the parts in the proboscis of *Laelaps echidninus* is clearly seen in the figure by Stanley (fig. 28 I), who says that a groove on the ventral surface of the "lingula" (labrum) extends into the mouth of the pharynx and probably aids in the flow of blood from the wound.

In longitudinal sections of the capitulum of Ixodides the labrum, of course, looks like a stylet, and in dissections the marginal membranes of the apical blade are sometimes lost entirely, so that the axial filament appears to be a slender rod projecting from the apex of the basal lobe, as it is usually shown in illustrations (fig. 28 E). Moreover, the end of the organ is often broken, and may be split,

which fact possibly explains Douglas' statement that the "stylet" of *Dermacentor andersoni* is "tripartite and quite short."

Above the basal lobe of the labrum is a flat pocket (figs. 27, 28 A, *Stv*) covered dorsally by the lower walls of the cheliceral sheaths. Into the inner end of this pocket open the ducts of the salivary glands (fig. 27, *SIDct*). The supralabial pocket thus serves as a salivarium, or receptacle for the saliva ejected from the ducts. Christophers (1906), however, regarded it as the "mouth cavity," and Nuttall, Cooper, and Robinson (1908) called it the "buccal cavity," which terminology has been followed by more recent writers. It is clear, however, that the space in question has no relation to the mouth or to the intake of food; it is appropriately named by Samson (1909) the "Speichelhöhle." The closure of the food canal of the hypostome by the labrum must exclude the saliva from direct entrance into the mouth; its only access to the food stream, then, would appear to be at the open distal part of the hypostomal gutter.

The flow of saliva from the salivarium pocket, according to Bertram (1939), is regulated by movements of the labrum ("tongue-like process"). The lumen of this organ in *Ornithodoros*, Bertram says, is a closed chamber, presumably filled with liquid, the posterior end of which extends into the pharynx against the anterior part of the dorsal wall of the latter, and therefore reacts to changes of pressure within the pharynx. The decreased pressure of the expanding pharynx contracts the labral chamber and deflates the labrum; conversely, contraction of the pharynx dilates the labrum. The alternate expansion and contraction of the labrum is thus supposed to exert a sucking action on the saliva entering the salivarium from the salivary ducts. A similar mechanism has not been observed by other writers.

The pharynx of the ticks presents no special features in its general structure. It is an elongate sack (fig. 28 A, *Phy*) surrounded by a thick layer of constrictor muscle fibers, within which the walls, when contracted, are thrown into three radial folds (*L, Phy*). Dilator muscles arise dorsally (*dld*) on the thickened lateral margins of the subcheliceral epistomal plate (*Epst*), and ventrolaterally (*dlv*) on the lower walls of the capitulum. In *Dermacentor variabilis* two winglike plates diverge laterally and posteriorly from the anterior end of the pharynx at the base of the labrum (fig. 28 D). The similar plates of *D. andersoni* are shown by Douglas (1943) to give attachment on their concave dorsal surfaces to flat muscles (*H*) inserted medially in the base of the labrum ("stylet"). The under surface of the labrum is produced into a toothlike process that fits into a groove of the lower wall of the entrance to the pharynx. This structure Douglas regards

as a pharyngeal valve, since contraction of the plate muscles would constrict the V-shaped oral aperture. The wing plates of the valve are said by Douglas to be extensions of the pharyngeal wall; the operative muscles, therefore, are evidently the anteriormost fibers of the dorsal constrictors of the pharynx.

*Trombidiformes*.—Among the trombidiform mites the chelicerae become progressively adapted for piercing by a transformation of the movable digits into hooks or stylets. In the larvae of the chiggers (Trombiculidae), which are parasitic on vertebrate animals, the cheliceral digits are hook-shaped with the points turned upward; they are used for cutting into the skin of the host, but the mite does not otherwise penetrate the skin. André (1927) says the chigger grasps the surface of the host with its palps, and then pushes the cheliceral hooks into the skin. From the puncture of the feeding chigger a tube-like structure extends into the flesh, which was formerly thought to be a sucking organ of the mite, and was named the "stylostome." Its formation, however, as described by André, is due to the injection of a digestive liquid by the chigger, which diffuses through the host tissue, producing the wall of the tube and an edematous condition surrounding the latter, especially at the inner end. Ewing (1944) says the host tissue in immediate contact with the injected fluid "is liquefied, and the adjoining tissue becomes toughened. As the predigested liquefied tissue (not blood) is sucked up by the mite and more digestive fluid is injected into the cavity thus produced there is formed a sclerotized tube which may be as long as the total length of the mite itself."

The water mites (Hydracnidae), which feed on the larvae of aquatic insects, have long, straight, styletlike cheliceral digits. The feeding and digestion of these mites has been fully described by Bader (1938), who says the mites seize the prey with the palps and tear a hole in the skin with the chelicerae. For from 10 to 20 minutes the mite then quietly holds on to the victim, during which time the congested salivary glands discharge their secretion into the body of the prey and the tissues of the latter are thereby dissolved. Sucking now begins and continues until the mite is replete or the prey is empty of its contents. An *Anopheles* larva, Bader says, can be sucked dry by three individuals of *Hygrobates longipalpus*, leaving nothing but the empty skin. After the preliminary digestion by the salivary secretion, the final digestion of the food, as in other Arachnida, according to Bader takes place intracellularly in the digestive cells of the capacious stomach and its large diverticula. Since these mites have no posterior opening to the alimentary canal, the waste products of digestion accumulate in the stomach cells.

Specialization of the feeding organs for piercing is carried farthest in the Tetranychidae, the members of which family, known as spider mites, are plant feeders. The movable digits of the chelicerae of the tetranychid mites are drawn out into long, slender stylets with recurved bases attached on the proximal segments of the chelicerae in such a manner that they are individually protractile and retractile. The basal segments of the chelicerae, however, are united with each other to form for the stylets a common support, which is itself protractile and retractile beneath an anterior fold of the dorsum of the body. The epistome and the hypostome compose a conical rostrum containing the mouth and the pharynx. The dorsal surface of the epistome is deeply grooved to form a channel in which the cheliceral stylets slide back and forth. The pharynx is cup-shaped, with the dorsal wall invaginated in the form of a plunger, activated by muscles arising on the epistome. Two pairs of silk glands open by a common duct into the distal end of the epistomal groove, and the duct of an unpaired salivary gland transverses the united cheliceral segments to open beneath them anteriorly. Closely associated with the chelicerae are the two spiracular apertures of the tracheal system, which lie medially in the infolded membrane just behind the united parts of the cheliceral bases. From each spiracle a long, finely ribbed, external groove, known as a "peritreme," extends posteriorly and laterally in the dorsal integument; inwardly the spiracles open into a pair of vertical respiratory tubes with thick sclerotic walls supported below on an apodeme of the epistome. From the lower ends of these tubes a large tracheal trunk is given off on each side, from which issue bundles of finer tracheae distributed anteriorly and posteriorly throughout the body.

The feeding organs of *Tetranychus telarius* (L.) have been described in detail by Becker (1935) and by Blauvelt (1945), but the terminology used by these writers is likely to give the uninformed student the impression that the feeding organs of the tetranychids have little relation to those of other Acarina, as indeed the unusual features of these mites themselves would seem at first sight to suggest. However, it is not difficult to fit the descriptions of Becker and Blauvelt into an interpretation entirely in accord with that given here of the acarine feeding organs in general.

A dorsal view of the forward part of the body of *Tetranychus* (fig. 29 A) shows anteriorly, projecting from beneath a flexible fold (*df*) of the back, what appears to be a broad, heart-shaped plate (*Stphr*) with a rounded outline in front and a deeply notched margin behind. This structure is commonly called the "mandibular plate."

since on its under surface are attached the recurved bases of the cheliceral stylets (*Stly*); but for this same reason there can be no question that it represents the united basal segments of the chelicerae, as said by Becker (1935) and by Vitzthum (1940-'43, p. 809), and

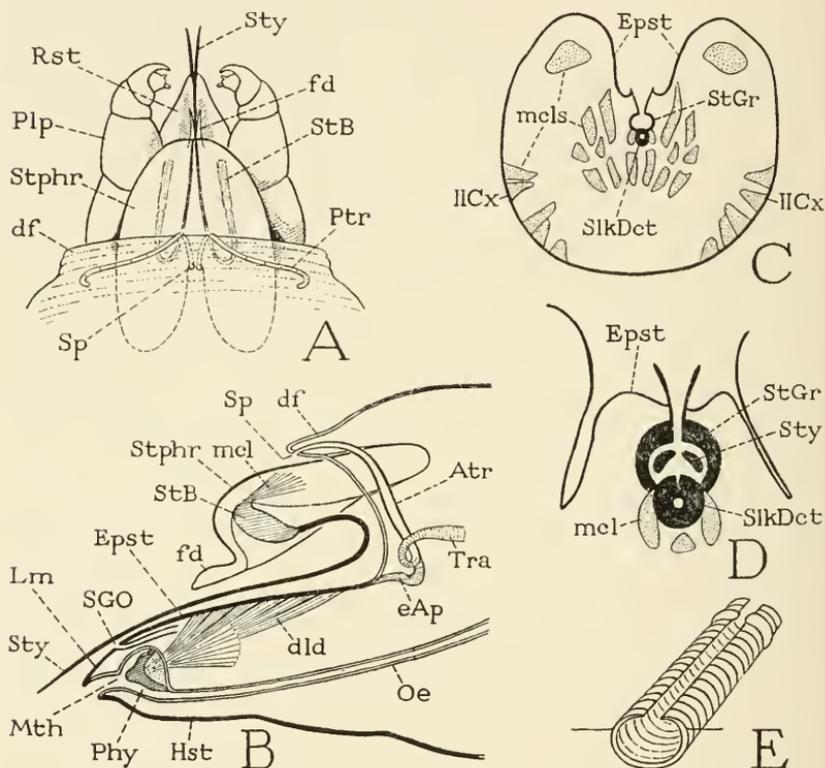


FIG. 29.—Acarina-Trombidiformes-Tetranychidae, *Tetranychus*.

A, dorsal view of capitulum and anterior part of body, showing the united cheliceral bases, or stylephore (*Stphr*), partly retracted beneath a marginal fold of the dorsum (*df*) covering the spiracles (*Sp*) and the infolded anterior ends of the peritremes (*Ptr*). B, diagrammatic interpretation of structure of feeding organs of *Tetranychus telarius* (L.) based on a lengthwise sectional figure by Blauvelt (1945, fig. 51), with parts somewhat separated for clarity of identification with corresponding parts of other Acarina. C, cross section of rostrum behind palps (from Blauvelt, 1945). D, cross section through stylet groove of epistome over the pharynx (from Blauvelt, 1945). E, piece of a pseudotracheal peritreme (from Blauvelt, 1945).

therefore might be termed more appropriately the "cheliceral plate," except for the fact that it is not a plate at all, but a thick lobe containing an extension of the haemocoel. The word *stylephore* (*Stphr*) suggests itself as a practical name. The rounded anterior surface of the stylephore is abruptly declivous (fig. 29 B) and bears ventrally

a pair of small thin processes (*fd*) that possibly represent the immovable cheliceral digits.

The cheliceral stylets (fig. 29 B, *Sty*) are attached apparently in deep anterior inflexions or pockets of the under surface of the stylophore (but the structure of the under surface of the stylophore as drawn in the diagram is somewhat conjectural). Each stylet has a flat pear-shaped base (*StB*) from which the strong but slender shaft extends first posteriorly and then loops downward and forward. On a projection of the stylet base, apparently dorsal to the articulation on the stylophore, is attached a group of muscle fibers (*mcl*), which, Blauvelt says, produce an up-and-down movement of the tip of the stylet. However, inasmuch as the stylets are closely held in the groove of the epistome (*D, Sty*), a downward rotation of their bases should cause a protraction of the shafts. Muscles antagonistic to the stylet protractors have not been observed, and it is possible that retraction results automatically from the elasticity of the stylets or of their basal connections. On the other hand, the principal movements of the stylets must be brought about by the protraction and retraction of the stylophore. The movements of the latter, according to Blauvelt, are produced by muscles from the dorsum of the body attached on the posterior lobes, and muscles attached distally in the stylophore that arise posteriorly on the vertical respiratory tubes. Both of these sets of muscles, however, would appear to be retractors, and it may therefore be supposed that, as in some other Acarina, protraction of the chelicerae is effected by a bulblike compression of the body.

The stylophore is capable of complete retraction beneath the marginal fold of the dorsum that ordinarily covers its basal half. This fold (fig. 29 A, B, *df*), projecting as it does over the cheliceral bases, possibly represents the tectum, or dorsal wall of the capitulum in other Acarina; if not, the tetranychid capitulum is incomplete dorsally, and is composed only of the coxal elements and the epistomal plate that unites their dorsal surfaces below the chelicerae, and forms the upper wall of the rostrum (B, *Epst*).

The rostrum (termed "hypostome" by Becker) projects as a short wide cone from between the bases of the palps (fig. 29 A, *Rst*). Its dorsal, or epistomal, wall is shown by Becker and by Blauvelt to form a trough (C, *Epst*) in which the stylophore ("mandibular plate") slides backward and forward. Along the bottom of the trough is a deep, thick-walled canal (C, D, *StGr*) that contains the shafts of the cheliceral stylets (D, *Sty*) and evidently serves to hold them in place during their functional activity. The common duct of the two pairs of silk glands runs beneath the stylet canal (C, D, *SlkDet*)

and, as already noted, opens into the distal end of the latter. If this duct represents the paired ducts of the salivary glands of the ticks that discharge above the base of the labrum (fig. 27, *SIDct*), the short apical part of the dorsal wall of the tetranychid rostrum projecting over the mouth may be referred to the labrum (fig. 29 B, *Lm*).

The hypostomal wall of the rostrum (*Hst*) is a simple ventral prolongation of the coxal region of the capitulum and has no appendicular accessories.

The mouth lies within the tip of the rostrum (fig. 29 B, *Mth*) and opens directly into the pharynx (*Phy*). The form of the tetranychid pharynx is unusual for a sucking apparatus, but is one characteristic of the salivary ejection pump of insects. By comparison with the tubular pharynx of other arachnids the cup-shaped sucking organ of *Tetranychus* is so short that the inflected dorsal wall takes the form of a thick conical plug with the dilator muscles (*dld*) from the epistome convergent upon its center. The oesophagus (*Oe*) proceeds in the usual manner from the posterior end of the pump chamber.

The respiratory system is an interesting feature of the tetranychid organization. Just why the spiracles should be in a place so inconvenient as the infolded membrane at the base of the united chelicerae is not clear (fig. 29 A, B, *Sp*), except that they are here by inheritance from prostigmatic ancestors. The so-called "peritremes" (*A*, *Ptr*), as above noted, are open channels of the integument that extend posteriorly and outward on the dorsal surface of the body from the spiracles. Their closely ribbed walls (*E*) give these channels a resemblance to tracheae, and, in fact, they might with better reason be termed *pseudotracheae* than are the similar canals on the mouth lobes of phalangiids and the labella of some Diptera that have to do with feeding and not with respiration. Blauvelt observes that the long, slitlike peritremes of *Tetranychus* give the spiracles access to the outer air at all usual positions of the chelicerae. It is evident that as they are pulled into the fold of integument over the cheliceral bases by the retraction of the latter, the indrawn parts of the canals are converted into closed tubes while the outer parts are still open to the air. When the cheliceral bases (stylophore) are fully retracted, however, Blauvelt says, the peritremes are completely shut off from the air, and this fact he points out "may explain in part the high degree of resistance of this mite to certain toxic gases such as hydrocyanic acid gas and nicotine vapor." The vertical respiratory tubes into which the spiracles open (fig. 29 B, *Atr*) are said to be enclosed in a common, strongly sclerotic wall, their ventral ends are supported on a median apodeme of the epistome (*eAp*), and the

tubes give attachment to retractor muscles of the chelicerae. These facts would suggest that the spiracular tubes are elongate atrial chambers, or secondary invaginations of the integument, rather than true tracheal trunks. From the lower end of each tube a large tracheal trunk (*Tra*) arises laterally, turns posteriorly, and gives off bundles of finer tracheae that aerate the entire body.

## ABBREVIATIONS USED ON THE FIGURES

(Other lettering explained in the legends.)

- aChS*, anterior cheliceral sheath.  
*An*, anus.  
*Ant*, antenna (*1Ant*, *2Ant*, first and second antenna).  
*Ap*, apodeme.  
*Atr*, spiracular atrium.
- Br*, brain.
- cAp*, coxal apodeme.  
*Chl*, chelicera.  
*ChlB*, cheliceral base.  
*chlF*, cheliceral foramen.  
*ChS*, cheliceral sheath.  
*Cp*, carapace.  
*cpr*, compressor muscle.  
*Ct*, cuticle.  
*Cuc*, cucullus.  
*Cx*, coxa (*IICx-VICx*, coxae of pedipalps and legs).  
*cxp*, coxal process of pedipalp.  
*cxr*, coxal ridge.
- D*, back of the body, dorsum.  
*Dac*, dactyl, median claw of pretarsus.  
*dc*, dorsal channel of pharynx.  
*Dct*, duct.  
*df*, fold of dorsum over bases of chelicerae.  
*dld*, dorsal dilator muscles of pharynx.  
*dll*, lateral dilator muscles of pharynx.  
*dvl*, ventral dilator muscles of pharynx.  
*dpl*, dorsal plate of pharynx.  
*dplcx*, dorsal plate of pedipalp coxa.  
*dpptar*, depressor muscle of pretarsus.  
*dpt*, depressor tendon.  
*dptar*, depressor muscle of tarsus.  
*dptb*, depressor muscle of tibia.
- eAp*, epistomal apodeme.  
*ccAp*, epistomocoxal apodeme.  
*ecs*, epistomocoxal sulcus.  
*Endst*, endosternum.
- Endt*, coxal endite (*IIEndt*, *IIIEndt*, *IVEndt*, coxal endites of pedipalps, first legs, and second legs).  
*Epst*, epistome (clypeus, subcheliceral plate).  
*Epth*, epithelium.
- f*, median frontal bar.  
*fc*, food canal.  
*fd*, immovable finger (fixed digit) of chelicera.  
*Fm*, femur.  
*FrG*, frontal ganglion.
- G*, ganglion (*IG*, tritocerebral ganglion, *IIG*, *IIIG*, ganglia of pedipalps and first legs).  
*GC*, genital chamber.  
*Gld*, gland.  
*GO*, genital opening.
- HL*, head lobe of embryo.  
*hs*, piece of skin of host drawn out in a papilla around the rostrum of ticks.  
*Hst*, hypostome.
- I-I'*, postoral somites (*I*, cheliceral somite).  
*iChS*, inner cheliceral sheath.
- L*, leg (*1L-4L*, first to fourth legs).  
*lbrmcl*, labral muscle.  
*lHcl*, labral haemocoelae.  
*li*, lamina inferior of pedipalp coxa.  
*Lm*, labrum ("lingula," "styletlike process").  
*lmd*, lamina dorsalis of preoral cavity.  
*lmv*, lamina ventralis of preoral cavity.  
*lpg*, lophognath.  
*ls*, lamina superior of pedipalp coxa.  
*lptar*, levator muscle of pretarsus.  
*lvt*, levator tendon.

- lvtar*, levator muscle of tarsus.  
*lvtb*, levator muscle of tibia.  
*mcl*, muscle.  
*Md*, mandible.  
*Ment*, mesenteron.  
*ml*, mouth lobe of Solpugida.  
*Mth*, mouth.  
*aChS*, outer cheliceral sheath.  
*Oe*, oesophagus.  
*Pat*, patella.  
*pChS*, posterior cheliceral sheath.  
*Pcr*, protocerebrum.  
*Pdp*, pedipalp (appendage of segment II).  
*pdpF*, foramen of pedipalp.  
*Phy*, pharynx.  
*Plp*, palp (telopodite of the pedipalp).  
*PrC*, preoral food cavity.  
*Prstm*, prestomum.  
*Ptar*, pretarsus.  
*Ptr*, "peritreme," pseudotracheal groove leading to spiracle.  
*Pvent*, proventriculus.  
*PvP*, proventricular pump.  
*Rst*, rostrum.  
*S*, sternum (*IS-IVS*, sterna of first four segments).  
*Ser*, serula.  
*SGO*, silk gland opening.  
*SIDct*, salivary duct.  
*SIGlds*, salivary glands.  
*SlkDct*, silk gland duct.  
*SoeG*, suboesophageal ganglion.  
*Sp*, spiracle.  
*Spn*, spinneret.  
*StGr*, stylet groove.  
*Stphr*, stylophore.  
*Sty*, stylet.  
*t*, tendon.  
*Tar*, tarsus (*1Tar*, *2Tar*, first and second tarsal subsegments, or tarsomeres).  
*Tb*, tibia.  
*Tect*, tectum capituli ("rostrum," "epistome").  
*tmcl*, transverse muscle.  
*tpg*, taphrognath.  
*Tr*, trochanter (*1Tr*, *2Tr*, first and second trochanters).  
*Tra*, trachea.  
*Un*, unguis, lateral claw of pretarsus.  
*V'Gld*, venom gland.  
*vpl*, ventral plate of pharynx.  
*V'Pr*, venom pore.

## REFERENCES

- ABRAHAM, N.  
 1923. Observations on fish and frog-eating spiders of Natal. *Ann. Natal Mus.*, vol. 5, pp. 89-94, pl. 7.
- ANDRÉ, M.  
 1927. Digestion "extra-intestinale" chez le rouget (*Leptus autumnalis* Shaw). *Bull. Mus. Nationale Hist. Naturelle*, vol. 33, pp. 509-516, 2 figs.
- ARTHUR, D. R.  
 1946. The feeding mechanism of *Ixodes ricinus* L. *Parasitology*, vol. 37, pp. 154-162, 15 figs.
- BADER, C.  
 1938. Beitrag zur Kenntnis der Verdauungsvorgänge bei Hydracarinaen. *Rev. Suisse Zool.*, vol. 45, pp. 721-806, 24 figs.
- BAERG, W. J.  
 1938. Tarantula studies. *Journ. New York Ent. Soc.*, vol. 46, pp. 31-43, 3 figs.
- BALFOUR, F. M.  
 1880. Notes on the development of the Araneina. *Quart. Journ. Micr. Sci.*, vol. 20, pp. 1-23, pls. 19-21.
- BARROIS, J.  
 1896. Memoire sur le developpement des Chelifer. *Rev. Suisse Zool.*, vol. 3, pp. 461-498, pls. 15-17.
- BARROWS, W. M.  
 1925. Modification and development of the arachnid palpal claw, with especial reference to spiders. *Ann. Ent. Soc. America*, vol. 18, pp. 483-516, pls. 35-43.
- BARTELS, M.  
 1930. Über den Fressmechanismus und chemischen Sinn einiger Netzspinnen. *Rev. Suisse Zool.*, vol. 37, pp. 1-42, 11 figs.
- BECKER, E.  
 1935. Die Mundwerkzeuge des *Tetranychus telarius* (L.) und deren Funktion in Beziehung zur chemischen Bekämpfung des letzteren. (In Russian, German summary.) *Rev. Zool. Russe*, vol. 14, pp. 637-654, 10 figs.
- BEIER, M.  
 1932. Pseudoscorpionida. In Kükenthal and Krumbach, *Handb. Zool.*, vol. 3, 2d half, pp. 117-192, figs. 157-267.
- BERLESE, A.  
 1897. Ricerche sugli organi e sulla funzione della digestione negli Acari. *Riv. Pat. Veg.*, vol. 5, pp. 129-195, 36 text figs., pls. 8, 9.
- BERNARD, H. M.  
 1893. Notes on some of the digestive processes in arachnids. *Journ. Roy. Micr. Soc.* for 1893, pp. 427-443, pl. 6.  
 1895. The comparative morphology of the Galeodidae. *Trans. Linn. Soc. London*, ser. 2, vol. 6, *Zool.*, pp. 305-417, pls. 27-34.

## BERTKAU, P.

1884. Über den Bau und die Funktion der sog. Leber bei den Spinnen. *Archiv mikr. Anat.*, vol. 23, pp. 214-245, pl. 12.

1885. Über den Verdauungsapparat der Spinnen. *Archiv mikr. Anat.*, vol. 24, pp. 398-451, pls. 20, 21.

## BERTRAM, D. S.

1939. The structure of the capitulum in *Ornithodoros*: a contribution to the study of the feeding mechanism in ticks. *Ann. Trop. Med. Parasitol.*, vol. 33, pp. 229-278, 22 figs.

## BLAUVELT, W. E.

1945. The internal morphology of the common red spider mite (*Tetranychus telarius* Linn.). *Cornell Univ. Agr. Exp. Stat., Mem.* 270, 35 pp. 11 pls.

## BONNET, A.

1907. Recherches sur l'anatomie comparée et le développement des Ixodidés. *Ann. Univ. Lyon, n.s.* 1, Fasc. 20, 180 pp., 104 text figs., 6 pls.

## BÖRNER, C.

1901. Zur äusseren Morphologie von *Koenenia mirabilis* Grassi. *Zool. Anz.*, vol. 24, pp. 537-556, 10 figs.

1902. Arachnologische Studien. V. Die Mundbildung bei den Milben. *Zool. Anz.*, vol. 26, pp. 99-109, 6 figs.

1904. Beiträge zur Morphologie der Arthropoden. I. Ein Beitrag zur Kenntnis der Pedipalpen. *Zoologica. Orig.-Abh. Ges. Zool.*, Heft. 42, Band 17, 5th and 6th Lief., 174 pp., 7 pls.

## BROWN, R. B.

1939. The musculature of *Agelena naevia*. *Journ. Morph.*, vol. 64, pp. 115-166, 12 pls.

## CHAMBERLIN, J. C.

1931. The arachnid order Chelonethida. *Stanford Univ. Publ. Biol. Sci.*, vol. 7, No. 1, 284 pp., 71 figs.

## CHRISTOPHERS, S. R.

1906. The anatomy and histology of ticks. *Sci. Mem. Officers of Med. and Sanit. Dep. of Gov. of India, n. s.*, No. 23, 55 pp., 6 pls.

## COOLEY, R. A., and KOHLS, G. M.

1944. The Argasidae of North America, Central America, and Cuba. *Monograph No. 1, Amer. Midland Nat.*, 152 pp., 57 text figs., 14 pls.

## CRONEBERG, A.

1888. Beitrag zur Kenntnis des Baues der Pseudoscorpione. *Bull. Soc. Imp. Nat. Moscou, n.s.* 2, pp. 416-461, 3 pls.

## DOUGLAS, J. R.

1943. The internal anatomy of *Dermacentor andersoni* Stiles. *Univ. California Publ. Ent.*, vol. 7, No. 10, pp. 207-271, 7 text figs., pls. 8-20.

## EWING, H. E.

1929. A synopsis of the American arachnids of the primitive order Ricinulci. *Ann. Ent. Soc. Amer.*, vol. 22, pp. 583-600, 3 pls.

1944. The trombiculid mites (chigger mites) and their relation to disease. *Journ. Parasitol.*, vol. 30, pp. 339-365, 7 figs.

## FRANK, H. R.

1938. Histologische Untersuchungen über die Verdauung bei Weberknechten. *Zeitschr. Morph. Ökol. Tiere*, vol. 33, pp. 151-164, 14 figs.

GERHARDT, U., and KÄSTNER, A.

1937. Araneae = Echte Spinnen = Webspinnen. *In* Kükenthal and Krumbach, *Handb. Zool.*, vol. 3, 2d half, pp. 394-656, figs. 484-854.

HAASE, E.

1890. Beiträge zur Kenntnis der fossilen Arachniden. *Zeitschr. deutsch. geol. Gesell.*, vol. 42, pp. 629-657, pls. 30, 31.

HANSEN, H. J., and SÖRENSEN, W.

1897. The order Palpigradi Thorell (*Koenenia mirabilis* Grassi) and its relationships to other Arachnida. *Ent. Tidskr.*, vol. 18, pp. 223-240, pl. 4.

1904. On two orders of Arachnida (Opiliones and Ricinulei), 182 pp., 9 pls. Royal Society of London.

HANSTRÖM, B.

1928. Vergleichende Anatomie des Nervensystems der wirbellosen Tiere, 628 pp., 650 figs. Berlin.

HENKING, H.

1882. Beiträge zur Anatomie, Entwicklungsgeschichte und Biologie von *Trombidium fuliginosum* Herm. *Zeitschr. wiss. Zool.*, vol. 37, pp. 553-663, pls. 34-36.

HEYMONS, R.

1901. Biologische Beobachtungen an asiatischen Solifugen nebst Beiträgen zur Systematik derselben. *Anh. Abhl. k. Preuss. Akad. Wiss.* for 1901, 65 pp.

1905. Über die Entwicklungsgeschichte und Morphologie der Solifugen. *Compt. Rend. 6th Internat. Congr. Zool. Bern, 1904*, pp. 429-436.

HOLMGREN, N.

1920. Zur Ontogenie der Stomodealbrücke bei den Spinnentieren. *Arkiv Zool.*, vol. 13, No. 1, 9 pp., 6 figs.

HUTTON, T.

1843. Observations on the habits of a large species of *Galeodes*. *Ann. Mag. Nat. Hist.*, vol. 12, pp. 81-85.

KARSCH, F.

1892. Über *Cryptostemma* Guér. als einzigen recenten Ausläufer der fossilen Arachnoideen-Ordnung der *Meridogastra* Thor. *Berliner ent. Zeitschr.*, vol. 37, pp. 25-32, pl. 4.

KÄSTNER, A.

1925. Die Nahrungsaufnahme einiger Phalangiden. *Zool. Anz.*, vol. 62, pp. 212-214, 1 fig.

1927. Pseudoscorpiones. *In* *Biologie der Tiere Deutschlands*, Lief. 25, pt. 18, pp. 1-65, 68 figs.

- 1932a. Pedipalpi Latreille. *In* Kükenthal and Krumbach, *Handb. Zool.*, vol. 3, 2d half, pp. 1-76, figs. 1-94.

- 1932b. Palpigradi Thorell. *In* Kükenthal and Krumbach, *Handb. Zool.*, vol. 3, 2d half, pp. 77-98, figs. 95-129.

- 1933a. Verdauungs- und Atemorgane der Weberknechte *Opilio parietinus* De Geer und *Phalangium opilio* L. *Zeitschr. Morph. Ökol. Tiere*, vol. 27, pp. 587-623, 27 figs.

- 1933b. Solifugae Sundevall. Walzenspinnen. *In* Kükenthal and Krumbach, *Handb. Zool.*, vol. 3, 2d half, pp. 193-299, figs. 268-362.

1935. Opiliones Sundevall-Weberknechte. *In* Kükenthal and Krumbach, *Handb. Zool.*, vol. 3, 2d half, pp. 300-393, figs. 363-483.

Kew, H. W.

1914. On the nests of pseudoscorpions: with historical notes on the spinning-organs and observations on the building and spinning of the nests. Proc. Zool. Soc. London for 1912, pp. 376-390.

KRAMER, P.

1876. Zur Naturgeschichte einiger Gattungen aus der Familie der Gamasiden. Arch. Naturg., vol. 42, pp. 46-105, pls. 4, 5.

LAURIE, M.

1890. The embryology of a scorpion (*Euscorpium italicus*). Quart. Journ. Micr. Sci., vol. 31, pp. 105-141, pls. 13-18.

LOCKWOOD, S.

1870. The horse foot crab. Amer. Nat., vol. 4, pp. 257-274, pl. 3.

McCLENDON, J. F.

1904. On the anatomy and embryology of the nervous system of the scorpion. Biol. Bull., Woods Holl, vol. 8, pp. 38-55, 13 figs.

MILLOT, J.

1931. Les glandes venimeuses des aranéides. Ann. Sci. Nat., ser. 10, Zool., vol. 14, pp. 113-147, 23 figs.

NUTTALL, G. H. F., COOPER, W. F., and ROBINSON, L. E.

1908. The structure and biology of *Haemaphysalis punctata*, Canestrini and Fanzago. Parasitology, vol. 1, pp. 152-181, pls. 12-16.

OETCKE, E.

1912. Histologische Beiträge zur Kenntnis der Verdauungsvorgänge bei den Araneiden. Zool. Jahrb., Zool., vol. 31, pp. 245-276, pl. 3.

PAVLOVSKY, E. N., and ZARIN, E. J.

1926. On the structure and ferments of the digestive organs of scorpions. Quart. Journ. Micr. Sci., vol. 70, pp. 221-261, 7 text figs., pls. 22, 23.

PETRUNKEVITCH, A.

1933. An inquiry into the natural classification of spiders, based on a study of their internal anatomy. Trans. Connecticut Acad. Arts Sci., vol. 31, pp. 299-389, 13 pls.

PLATEAU, F.

1877. Recherches sur la structure de l'appareil digestif et sur les phénomènes de la digestion chez les Aranéides dipneumones. Bull. Acad. Roy. Sci., Belgique, ser. 2, vol. 44, pp. 129-181, 323-355, 477-531, 3 pls.

POCOCK, R. I.

1902. On some points in the anatomy of the alimentary and nervous systems of the arachnid Suborder Pedipalpi. Proc. Zool. Soc. London for 1902, vol. 2, pp. 169-188, 6 figs.

POLICE, G.

1927. Sull'apparato bucco-faringeo del *Phalangium opilio* L. Boll. Soc. Nat. Napoli, ser. 2, vol. 19, pp. 280-361, pls. 18, 19.  
1928. L'apparato buccofaringeo dei Galeodi. Ann. Mus. Zool. Univ. Napoli, n.s., vol. 5, No. 19, 25 pp., 6 figs.

PÖRTMAN, R. W., and DALKE, P. D.

1945. Infestation of a red fox by *Amblyomma americanum*. Journ. Econ. Ent., vol. 38, No. 3, p. 397.

REESE, A. M.

1944. The anatomy of the venom glands in the black widow spider, *Latrodectus mactans*. Trans. Amer. Micr. Soc., vol. 63, pp. 171-174, 1 pl.

## REUTER, E.

1909. Zur Morphologie und Ontogenie der Acariden, mit besonderer Berücksichtigung von *Pediculopsis graminum* (E. Reut.). Acta Soc. Sci. Fennicae, vol. 36, No. 4, 287 pp., 6 pls.

## ROBINSON, L. E., and DAVIDSON, J.

- 1913, '14. The anatomy of *Argas persicus* (Oken 1818). Parasitology, vol. 6, pp. 20-48, 217-256, 382-424, pls. 1-5, 14-17, 25-28.

## ROESLER, R.

1934. Histologische, physiologische und serologische Untersuchungen über die Verdauung bei der Zeckengattung *Ixodes*, Latr. Zeitschr. Morph. Ökol. Tiere, vol. 28, pp. 297-317, 17 figs.

## ROEWER, C. F.

1936. Chelonethi oder Pseudoskorpiones. In Bronns Klassen und Ordnungen des Tierreichs, vol. 5, Abt. 4, Buch 6, 1st Lief., pp. 1-160, figs. 1-155.

## RUCKER, AUGUSTA.

1901. The Texan *Koenenia*. Amer. Nat., vol. 35, pp. 615-630, 6 figs.  
1903. Further observations on *Koenenia*. Zool. Jahrb., Syst., vol. 18, pp. 401-434, pls. 21-23.

## SAMSON, KATHARINA.

1909. Zur Anatomie und Biologie von *Ixodes ricinus* L. Zeitschr. wiss. Zool., vol. 93, pp. 185-236, 18 text figs., pls. 9-12.

## SCHLOTTKE, E.

- 1933a. Darm und Verdauung bei Pantopoden. Zeitschr. mikro-anat. Forsch., vol. 32, pp. 633-658, 14 figs.  
1933b. Der Fressakt des Bücherskorpions (*Chelifer cancroides* L.). Zool. Anz., vol. 104, pp. 109-112, 2 figs.  
1934. Histologische Beobachtungen über die intrazelluläre Verdauung bei *Dendrocoelum lacteum* (Müll.) und *Euscorpium carpathicus*. Sitzungsab. nat. Ges. Rostock, ser. 3, vol. 4, pp. 76-86, 3 figs.  
1935. Biologische, histologische und physiologische Untersuchungen über die Verdauung von *Limulus*. Zeitschr. vergl. Physiol., vol. 22, pp. 359-413, 28 figs.  
1936. Über die Verdauungsfermente der Vogelspinnen. Sitzungsab. nat. Ges. Rostock, ser. 3, vol. 6, pp. 89-106.

## SCHULZE, P.

1932. Über die Körpergliederung der Zecken, die Zusammensetzung der Gnathosoma und die Beziehung der Ixodoidea zu dem fossilen *Anthracomarti*. Sitzungsab. nat. Ges. Rostock, ser. 3, vol. 3, pp. 104-126, 21 figs.  
1935. Zur vergleichenden Anatomie der Zecken. Zeitschr. Morph. Ökol. Tiere, vol. 30, pp. 1-40, 37 figs.

## SEN, S. K.

1935. The mechanism of feeding in ticks. Parasitology, vol. 27, pp. 355-368, 15 figs.

## SHARIF, M.

1928. A revision of the Indian Ixodidae with special reference to the collection in the Indian Museum. Rec. Indian Mus., vol. 30, pp. 217-344, 49 text figs., pls. 8, 9.

SÖRENSEN, W.

1914. Recherches sur l'anatomie, extérieure et intérieure, des Solifuges. Overs. Kong. Danske Vid. Selsk. Forh., 1914, No. 3, pp. 131-215, 2 pls.

STANLEY, J.

1931. Studies on the musculatory system and mouth parts of *Laelaps echidninus* Berl. Ann. Ent. Soc. Amer., vol. 24, pp. 1-12.

STEDING, ELISABETH.

1924. Zur Anatomie und Histologie von *Halarachne Otariae* n. sp. Zeitschr. wiss. Zool., vol. 121, pp. 442-493, 42 text figs., pls. 1-4.

STÖRMER, L.

1944. On the relationships and phylogeny of fossil and recent Arachnomorpha. Skrift. Norske Vidensk.-Akad. Oslo, vol. 1, Mat.-Naturv. Kl., No. 5, 158 pp., 29 figs.

THON, K.

1906. Die äussere Morphologie und die Systematik der Holothyriden. Zool. Jahrb., Syst., vol. 23, pp. 677-724, pls. 28, 29.

TOTZE, R.

1933. Beiträge zur Sinnesphysiologie der Zecken. Zeitschr. vergl. Physiol., vol. 19, pp. 110-161, 38 figs.

TRUE, G. H.

1932. Studies of the anatomy of the Pajaroello tick, *Ornithodoros coriaceus* Koch. I. The alimentary canal. Univ. California Publ. Ent., vol. 6, pp. 21-48, 17 text figs., pls. 4-6.

TULK, A.

1843. Upon the anatomy of *Phalangium Opilio* (Latr.). Ann. Mag. Nat. Hist., vol. 12, pp. 153-165, 243-253, 318-331, pls. 3-5.

VERSLUYS, J., and DEMOLL, R.

1920. Die Verwandtschaft der Merostomata mit den Arachnida und den anderen Abteilungen der Arthropoda. Proc. Kon. Akad. Wetens. Amsterdam, vol. 23, pp. 739-765, 6 figs.

VITZTHUM, H. G.

- 1940-'43. Acarina. In Bronns Klassen und Ordnungen des Tierreichs, vol. 5, pp. 1-1011, 498 figs.

WAGNER, J.

1894. Die Embryonalentwicklung von *Ixodes calcaratus* Bir. Trav. Soc. Nat. St. Pétersbourg, Zool., vol. 24, Livr. 2, 246 pp., 4 pls.

WARREN, E.

1923. Note on a lizard-eating S. African spider. Ann. Natal Mus., vol. 5, pp. 95-100, 1 fig.

WHEELER, W. M.

1900. A singular arachnid (*Koecenia mirabilis* Grassi) occurring in Texas. Amer. Nat., vol. 34, pp. 837-850, 4 figs.

WINKLER, W.

1886. Anatomie der Gamasidae. Arb. Zool. Inst. Univ. Wien, vol. 7, pp. 317-354, 5 pls.

WIRÉN, E.

1918. Zur Morphologie und Phylogenie der Pantopoden. Zool. Bidrag, Uppsala, vol. 6, pp. 41-181, 40 text figs., pls. 9-16.

WITH, C. J.

1904. The Notostigmata, a new suborder of Acari. Videnskab. Medd. Naturhist. Foren. Kjöbenhavn, vol. 56, pp. 137-192, pls. 4-6.